Moult speed predicts pairing success in male harlequin ducks

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Abstract. The bright plumage of male ducks in sexually dichromatic species is thought to have evolved through intense sexual selection. This study examined the relationship between the timing and speed of moult into this bright plumage and subsequent mating success of male harlequin ducks, *Histrionicus histrionicus*. Males that moulted relatively slowly had a lower chance of establishing a pair bond than others. The timing of moult was unrelated to whether a male obtained a mate. Moult speed and timing were not correlated within individual males, but were significantly repeatable in individual males over 2 years. Moult speed probably reflects the condition of males, whereas timing of moult is more likely to be related to the distance to an individual's breeding area, which determines the timing of arrival to the moulting grounds. In waterfowl species that have been studied, males usually form dominance hierarchies before pairing and females tend to choose dominant males. We suggest that male harlequin ducks that moult slowly are poor-quality individuals, which are relegated to subordinate status and are unlikely to attract a mate the following autumn.

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The conspicuous plumage of male ducks in sexually dichromatic species has been cited as an example of sexual selection for bright coloration (Darwin 1871; Lack 1974). Waterfowl species with life-long pair bonds are generally monochromatic, whereas serially monogamous species are highly dichromatic (Scott & Clutton-Brock 1989). A significantly male-biased sex ratio in duck populations (Sargeant & Raveling 1992) has presumably led to strong sexual selection and the evolution of bright plumages.

Ducks tend to form pair bonds well in advance of the breeding season (Rohwer & Anderson 1988) and the pair bond ends sometime during incubation, after which males depart to initiate their moult. Males do not provide any parental care except in some Southern Hemisphere species (McKinney 1985). Thus, females probably choose males based on phenotypic qualities that reflect either their genetic quality, which can be passed on to the offspring, or the males' quality as a mate, such as their ability to protect females from other males allowing her to feed uninterrupted. Paired females are harassed less by males than unpaired females and are able to increase their foraging rates during winter and spring (Ashcroft 1976). High-quality males are also able to defend their female from harassment during nesting leading to more successful nesting (Sorenson 1992).

In waterfowl, as in many birds species, females prefer brightly adorned males (see Andersson 1994), perhaps because males with the brightest plumages are in the best condition (Hill & Montgomerie 1994). Female ducks also prefer males that have all of their alternative (breeding) plumage characters fully developed (Klint 1980; Weidmann 1990; Omland 1996a). Paired males collected in the wild have a more complete development of their alternative plumage than unpaired males (Hohman & Ankney 1994). Furthermore, adult males tend to have fully developed breeding plumages, whereas yearling males sometimes do not completely develop this plumage or the development is delayed until courtship has already begun, putting them at a disadvantage

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(Wishart 1983; Hepp 1988). Therefore, the timely acquisition of a complete alternative plumage is important for male ducks attempting to find a mate.

We initiated a study to determine the relationship between the speed (or rate), timing (or onset) of moult and the subsequent pairing success of males in a wild population of harlequin ducks, *Histrionicus histrionicus*. In this study we have sufficient observations of known individuals to document the relative speed and timing of their wing, tail, and pre-basic and pre-alternate body feather moult, and, their subsequent pairing success the following autumn. We conclude by discussing possible factors that influence moulting speed and timing, and potential reasons why females may choose these characters, given the life history of this species.

METHODS

Study Species

Harlequin ducks are small (500–700 g) sea ducks that nest along lowland, sub-alpine and alpine streams and winter on coastal, rocky shorelines (Palmer 1976). Harlequin ducks are highly dimorphic, with males having a variety of striking plumage characters. The general body plumage for the males is a dark blue merging to a slate grey on the belly. They also have large white crescents behind the bill and on the neck, two large white bands bordered by black under the neck and chest, white tertials and scapulars, rich navy blue secondaries, and chestnut coloured feathers on the flanks. Females, on the other hand, are generally brown with white bellies streaked with brown. Both sexes have a white patch behind the bill and a circular white patch behind the eye.

Males return to the non-breeding ground beginning in mid-June to July, and females return in August–September (Robertson et al. 1997). Males begin to moult as soon as they arrive on the non-breeding grounds, and most males have completed moulting by the end of September (Robertson et al. 1997). Pair bonds begin to form in October and are maintained through the following spring when the pairs migrate to breeding locations (Gowans et al. 1997). Pairs tend to reunite (as defined in Rowley 1983) if both members of the pair return from the breeding grounds to the same wintering location (Gowans et al.

1997). Many harlequin ducks moult and over-winter at the same location, an uncommon trait among waterfowl.

Study Area and Field Methods

This study was conducted from July 1994 to May 1997 near White Rock, in coastal southwestern British Columbia. The study site comprised a 5.5-km stretch of rocky shoreline where up to 150 harlequin ducks spend the non-breeding season. Each year, male harlequin ducks were captured in late July while they were flightless. The drakes were rounded up with sea kayaks and corralled into funnel traps. Individuals were sexed and aged (yearling or adult) by measuring the depth of the bursa of Fabricius during cloacal examination (Peterson & Ellarson 1978). It is not possible to catch juveniles with this technique because they do not moult their flight feathers in their first year. All birds were measured, weighed and banded with standard USFWS bands and a plastic tarsal band with a unique two letter-number code. Individuals were released in small groups after processing.

Observations of marked birds were carried out throughout the non-breeding season. During the moulting period (June–September), observations were made once or twice a week. Harlequin ducks often haul out on to rocks to preen and rest, and at this time the leg bands are clearly visible. Individual males were seen between three and 17 times during the moulting period. When an individual male was identified, we assessed the stage of his moult. Drakes undergo two body moults and one wing (primaries and secondaries) and tail moult per year. The first (pre-basic) body moult after breeding leads into a basic (eclipse) plumage in which the male is generally drab and female-like. While in basic plumage, the remiges (wing feathers) and rectrices (tail feathers) are shed and replaced. Males remain in basic plumage for an average of 52 days (Cooke et al. 1997), then undergo a pre-alternate body moult during which they acquire a new alternative (breeding) plumage. Tertial feathers in waterfowl are moulted as body feathers and are replaced twice a year (Stresemann & Stresemann 1966). Basic tertials have white ovals on them that are visible in the field. They are grown and then lost just before the pre-alternative moult begins. Tertials in the alternative plumage are the very last visible

feathers to grow in and their length can be visually assessed at the end of the pre-alternative moult (Cooke et al. 1997). For the purposes of this paper we define the moulting period as the time when males begin the pre-basic moult to the time they complete the pre-alternative moult. This entire moulting sequence lasts approximately 3 months in individual harlequin ducks (Cooke et al. 1997).

Males were categorized into a sequence of stages during moult. These stages were: (1) still in old alternative plumage; (2) just beginning the pre-basic body moult; (3) undergoing the pre-basic body moult; (4) just finishing the pre-basic body moult; (5) in basic plumage; (6) in basic plumage with no primaries; (7) in basic plumage with primaries and basic tertials one-quarter, one-half, three-quarters or full grown; (8) in basic plumage with no basic tertials; (9) just beginning the pre-alternative body moult; (10) undergoing the pre-alternative body moult; (11) just finishing the pre-alternative body moult; and finally (12) in alternative body plumage with alternative tertials one-quarter, one-half, three-quarters and full grown. It was not necessary to use the tail moult to identify moult stages as tail feather re-growth matches the initiation of the pre-alternative moult. This entire sequence of moulting is consistent among all harlequin ducks studied to date (G. J. Robertson, unpublished data), and follows the general pattern seen in ducks (Palmer 1976).

The population was monitored throughout the following autumn, winter and spring to determine whether males were successful in obtaining a mate. Pairs were easily identified after observing individuals for 5–10 min. Generally, pairs moved synchronously and males vigorously defended their mates from intruding males (Gowans et al. 1997). Unpaired males formed small groups and were seen over a wider range of sites in the study area. The pairing status of an individual was considered confirmed if the individual was seen in that state more than three times. It was not possible to determine whether all males successfully paired because some left the study site after moulting.

Statistical Analyses

To partition moult into its two temporal components (timing and speed) and to cope with the problem of not sighting all males on any given survey, we chose a method of analysis that compares the moult stage of each and every male to all the other males seen on the same survey day. For each survey day, each male was ranked by his stage of moult and this rank was subtracted from the rank of all of the other males seen that day. This difference in rank was entered into a matrix that included rank differences for all other males on each survey day. To compare the relative moult speeds of males, we analysed all data matrices in which a particular male was seen in a repeated measures design (PROC MIXED, SAS Institute 1996), the repeated measure being all of the other males against which a particular male was compared. Date was treated as a continuous variable, and regressed in this design with the difference in ranks between males as the dependent variable. A significant positive regression slope indicated that a male was gaining rank over time as compared with the other males in the data set. These males were identified as 'fast' moulting males. Similarly, males with significant negative slopes were identified as 'slow' moulters. All other males were identified as 'average' speed moulters. This method does not give an actual rate of moulting in terms of feather growth per day, but rather an index of moult speed relative to all other males.

To estimate the relative timing of moult we used the least-squares mean rank calculated from the above analyses as an index of the relative timing of moult for each male. Because males arrive and begin moulting at different dates, a least-squares mean rank controls for this variation and calculates an expected mean rank at the same date for all males. A least-squares mean can be considered to be calculated at the mean of the independent variable (date in this case), therefore, this value does not describe an actual date when moult was initiated but rather provides a comparison among males of the relative timing of moult. Positive values reflect earlier moulting, negative values represent later moulting.

We calculated repeatabilities for moult speed and moult timing following Lessells & Boag (1987). We used non-parametric tests to compare moult speed and timing because the data for these variables were limited and generally not normal. Many of the same males were used in the analyses in both years ($N=13$) because pairs tend to reunite if both members return to the study site (Gowans et al. 1997). Therefore, the data between the 2 years were pseudoreplicated for a portion of the

males. However, the data were not pooled over the 2 years. As such, the analyses for the 2 years should not be considered two independent tests, but neither are they completely pseudoreplicated. Three males did change pairing status from one year to the next.

RESULTS

Moulting Speed and Pairing Success

Some males moulted significantly slower or faster than other males in the population. Of 35 males identified during the moult in 1995, 13 had significant positive slopes (they gained rank over time), 14 had slopes not significantly different from zero, and eight had significant negative slopes. We were able to determine whether 26 of these males subsequently paired the following spring. Seven of eight fast-moulting males (87.5%), and 10 of 12 average-speed moulting males (83.3%) successfully paired, but only two of six slow-moulting males (33%) were able to successfully attract mates. Hence, fewer slow-moulting males were successful in obtaining a mate than all other males (Fisher's exact test: $P=0.028$).

Of 38 males identified in 1996, 10 males moulted faster than the others, 19 moulted at average speeds and nine moulted slower than the other males. Twenty of these males were subsequently sighted and we were able to determine whether they were paired. Seven of eight fast-moulting males (87.5%) and four of six average-speed moulting males (66.6%) successfully paired, but only one of six slow-moulting males (16.6%) was able to attract a mate successfully. Fewer slow-moulting males were successful in obtaining a mate than all other males (Fisher's exact test: $P=0.018$). Paired males moulted significantly faster than unpaired males in both years (Wilcoxon paired-rank test: 1995: $Z_{19,7}\approx2.17$, $P=0.030$; 1996: $Z_{12,8}\approx2.04$, $P=0.041$; Fig. 1).

Moult Timing and Pairing Success

The timing of moult did not differ between paired and unpaired males in either year (Wilcoxon paired rank test: 1995: $Z_{19,7}\approx1.67$, $P=0.091$; 1996: $Z_{12,8}\approx1.20$, $P=0.23$; Fig. 1). In a step-wise logistical regression with pairing status (paired and unpaired) as the dependent variable,
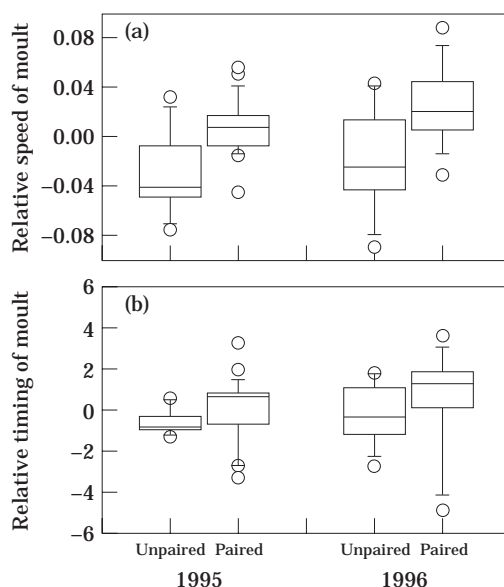

Figure 1. Box plots showing distributions of (a) relative moult speed and (b) timing of unpaired and paired male harlequin ducks. The edges of each box represent 25th and 75th percentiles, error bars the 10th and 90th percentiles, and the line in the middle of each box is the median. See text for sample sizes and statistics.

moult speed entered and remained in the model as a significant explanatory variable (1995: Wald $\chi_1^2=3.86$, $P=0.049$; 1996: Wald $\chi_1^2=3.98$, $P=0.046$). Moult timing did not enter the model in either year ($P>0.05$).

Repeatabilities and Correlations between Moult Speed and Timing

Both the speed of moulting (repeatability=0.35, $F_{25,26}=2.06$, $P=0.036$) and the timing of moulting (repeatability=0.51, $F_{25,26}=3.06$, $P=0.004$) were significantly repeatable within males over the 2 years. However, moulting speed and timing were not significantly correlated in either year (Spearman rank correlations: 1995: $r_{26}=-0.034$, $P=0.87$; 1996: $r_{25}=-0.21$, $P=0.30$).

DISCUSSION

Wild male harlequin ducks that moulted slower than other males were less likely to obtain a mate the subsequent winter. The timing of moult,

however, was not related to mating success, nor were moult speed and timing correlated.

Speed of Moult

Moult speed may reflect an individual's body condition or phenotypic quality. Plumage quality has been shown to be positively related to nutritional condition and moulting speed in house finches, *Carpodacus mexicanus* (Hill & Montgomerie 1994) and barn swallows, *Hirundo rustica* (Møller et al. 1994). Furthermore, plumage quality is also related to mating success in these species (Hill 1990; Møller 1994). This evidence indirectly suggests that moulting speed may be a good indicator of condition in birds. Murphy et al. (1988) documented that white-crowned sparrows, *Zonotrichia leucophrys*, fed poor-quality diets re-grew their feathers more slowly, moulted fewer feather tracts simultaneously and developed a poorer-quality plumage at the end of the moult. Male mallards, *Anas platyrhynchos*, fed on low-protein diets did not moult their remiges more slowly than mallards fed a high-quality diet, but their new wing feathers were shorter (Pehrsson 1987). These two studies are not necessarily contradictory as there are two methods for a bird to increase the speed of moult. One is to grow individual feathers faster, the other is to moult more feather tracts at the same time. We believe that the second method is the more likely explanation of variation in speed of moult in harlequin ducks. Studies of waterfowl show that feather growth rates are remarkably constant, and are probably at a physiological maximum (Hohman et al. 1992). There appears to be more flexibility in the number of feather tracts birds can moult simultaneously than in the rate at which feathers grow (Newton 1967; Murphy & King 1984), although adjustments to both can occur in some species (Hahn et al. 1992).

Plumage quality is correlated with dominance in some male ducks (Brodsky et al. 1988; Holmberg et al. 1989). Both female choice and male–male competition appear to play a role in pair formation in duck populations (McKinney 1987). In most duck species studied to date, males form dominance hierarchies (Hepp 1988) and females subsequently choose among these males (Wishart 1983), although Sorenson & Derrickson (1994) showed that males became dominant after they were chosen by a female. Males that were restricted in their access to food were less active in courtship activities (Brodsky & Ankney 1985; Hepp 1988; Holmberg et al. 1989); therefore, males in good condition may be able to display more and achieve a higher dominance ranking. Generally, female ducks preferred males that courted at the highest rate, had a high dominance ranking, and had the best-quality plumage and ornaments (Holmberg et al. 1989; Sorenson & Derrickson 1994; Omland 1996b).

We suggest that male harlequin ducks that can readily meet the nutritional requirements and/or metabolic costs of moulting do so quickly. These males may also be vigorous in establishing themselves in the dominance hierarchy and be better able to attract females. We were not able to quantify differences in plumage quality, because males appeared to us to have very similar plumages. We did notice two yearlings that had poorly coloured chestnut flanks, the major red/orange portion of the plumage. Neither was successful in obtaining a mate. However, another yearling male moulted quickly and successfully paired, so our observations do not appear to be a simple age effect.

The repeatability of moult speed is interesting as it may reflect some inherent physiological differences in the ability of males to moult. Alternatively, males may tend to achieve the same body condition each summer and autumn during the moult due to behavioural interactions. Male harlequin ducks form large groupings during the moulting period and we have postulated that males may be establishing a hierarchy during this period (Cooke et al. 1997), as observed in many other duck species (McKinney 1992). Because males are philopatric to their moulting sites (G. J. Robertson, unpublished data) many of the same individuals interact year after year. Males that are of low status in one year may be unable to rise in the hierarchy and thus remain low in status year after year. Unlike the well studied ducks in the genus *Anas* (McKinney 1992), behavioural interactions among harlequin ducks are relatively rare and non-aggressive. Very little agonistic behaviour among males is apparent during the moulting period (G. J. Robertson, unpublished data). Furthermore, males feed very little during this time, suggesting that they are not under any great nutritional stress. Finally, foraging habitat, at least at our study site, is distributed more or less evenly, making it very difficult for dominant males

to restrict the foraging opportunities of other birds. Unfortunately, behavioural interactions among males are so rare it would be very difficult to assess the dominance ranking of males directly.

Timing of Moult

The timing of moult was not related to the success of males in finding a mate. Individuals from the same wintering grounds breed at many different locations (R. I. Goudie, unpublished data). Males whose mates breed in the coastal mountain streams potentially initiate nesting almost 6 weeks before females nesting in the Rocky Mountains. There is considerable variation in the arrival times of harlequin ducks to the non-breeding grounds (Robertson et al. 1997), and males begin moulting as soon as they arrive on the non-breeding grounds (Cooke et al. 1997). Thus, the timing of moult in this population is probably a better indicator of breeding location rather than male quality. This contrasts with observations for house finches, barn swallows and superb fairy-wrens, *Malurus cyaneus*, in that early-moulting males of these species tend to moult into showier plumages and subsequently achieve a higher mating success (Hill & Montgomerie 1994; Møller et al. 1994; Mulder & Magrath 1994). Additionally, mallards fed high-protein diets moulted into their basic plumage moult earlier than birds fed low-protein diets (Pehrsson 1987). Because the entire moulting process takes a long time (3 months) in harlequin ducks, all males may begin moulting immediately on their return to the non-breeding grounds to be ready for courtship in September and October. The high repeatability of moult timing is probably a function of the high female breeding philopatry of harlequin ducks (Bengtson 1972) and the tendency of pairs to re-unite year after year (Gowans et al. 1997), so males are returning to the same breeding location year after year.

Conclusion

We have documented a relationship between pairing and moulting speed in harlequin ducks. Most females are not present while the males are moulting intensively (Robertson et al. 1997), so they cannot assess male moult speed directly. Females are probably choosing one or more other characters also correlated with male quality, poss-ibly the dominance of the male with respect to others, plumage quality and/or the quality of male displays. Females choosing good-quality males may be choosing good genes for their offspring via honest advertisement (Pomiankowski 1987) and/or choosing a male that will actively rebuke suitors and allow the female to feed undisturbed; this latter choice being a case of the good parent process of sexual selection (Hoelzer 1989).

In waterfowl, female body condition during the winter and especially in the spring is important in determining subsequent reproductive success in the following summer (Alisauskas & Ankney 1992). Females selecting dominant males as mates will have better access to resources during a time when nutrients for reproduction are being accumulated (Ashcroft 1976; Paulus 1983). Thus a female's fecundity is determined, in part, by the quality of her male. Females selecting males that possess traits reflecting good body condition and vigour will be at an advantage, leading to female choice for these traits and an increased reproductive success (Hepp 1984).

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