

Pairing Decisions in the Harlequin Duck: Costs and Benefits

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Abstract.—In waterfowl, the male costs and female benefits hypothesis considers that the timing of pairing will depend on the balance between the costs and benefits for each sex. Females may benefit by increasing their access to food and social status, and by decreasing harassment from conspecifics, while maintaining a pair bond for a long period should be costly to males. To investigate costs and benefits of early pairing in the Harlequin Duck (*Histrionicus histrionicus*), we compared time budgets and frequency of interactions (agonistic, courtship, and mate guarding behavior) from paired and unpaired males and females. A total of 400 thirty-minute focal-animal sampling sessions were used for the analysis. Overall, feeding time did not differ between paired and unpaired birds of both sexes. However, regardless of their reproductive status, females spent about 15% more time feeding than males throughout the winter. While diving, paired males spent 4% less time underwater than unpaired males, but no difference was found between paired and unpaired females. Males spent more time on the surface between dives than females, yet the differences between paired and unpaired birds were not significant. Paired males were engaged in more interactions (mainly mate guarding) than unpaired males. Interactions received by paired and unpaired females did not differ overall, however, from late October to early May, interactions with paired females decreased, while interactions directed to unpaired females increased. Thus the pair bond, though being apparently costly to males, did not obviously benefit females by increasing feeding time. Early pairing in the Harlequin Duck may result from other factors, such as the advantages that pair reunion may confer. *Received 9 September 2001, accepted 2 February 2002.*

Key words.—Foraging behavior, pair formation, Harlequin Duck, *Histrionicus histrionicus*, time budgets.

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Pair bonds are established shortly before breeding in most bird species, whereas in contrast, most migratory ducks pair on the wintering grounds. In waterfowl, parental investment is typically biased towards females, and operational sex ratios are male biased (Owen and Dix 1986). It has been suggested that, for species that pair during the winter, the actual timing of pairing will depend on the balance between the costs and benefits for each sex; females favor winter pairing to increase their ability to breed early and to increase their feeding efficiency, while males benefit by assuring the acquisition of a mate (Spurr and Milne 1976; Paulus 1983; Rohwer and Anderson 1988).

The male costs and female benefits hypothesis considers that early pairing could benefit females by increasing their social status, access to food, and by mate guarding; assuming that mate guarding decreases

harassment from conspecifics (Rohwer and Anderson 1988). In contrast, maintaining a pair bond could be energetically costly to males, in particular mate guarding or territory defense. Male-male competition will favor early pairing, especially if the operational sex ratio is male-biased and if pairing occurs during an extended period of time; then the risks for a male to remain unpaired will increase as the season progresses. Additionally, the earliest pairing individuals may be the best quality individuals (Afton 1984; McKinney 1986), and early pairing may allow females to evaluate the quality of the mate for a longer period of time. If females derive benefits from being paired, they should favor early pairing, whereas males should delay the time of pairing to a point where the risks of remaining unpaired and the possibility of obtaining a high quality female counterbalance the costs of maintaining a pair bond for a longer period of time.

The ability to pair earlier and maintain a pair bond for a long period of time varies within individuals of the same population. For example, American Black Duck (*Anas rubripes*) males in good condition pair earlier than males in poorer condition (Brodsky and Weatherhead 1985; Hepp 1986). Experimental manipulation of body condition of male Mallard (*Anas platyrhynchos*) showed that females only courted males in better condition, and among them, females preferred individuals with high status in social display and plumage characteristics, intermediate age, and small body size (Holmberg *et al.* 1989).

Harlequin Ducks (*Histrionicus histrionicus*) form pair bonds on the wintering grounds (Gowans *et al.* 1997; Robertson *et al.* 1998). These seabirds are monogamous. Males desert the breeding area after the clutch is completed and females incubate and attend the brood. Harlequin Ducks are faithful to the wintering area and pair with the same mate in subsequent years (Bengtson 1972; Robertson *et al.* 1998; Robertson and Cooke 1999). In a study with individually banded birds, when both members of a pair returned to the same wintering area, all 36 pairs reformed (Smith *et al.* 2000). The actual timing of pair formation varies substantially in this species. Pair formation occurs from the end of pre-alternate molt (September) until spring departure, with re-uniting of pairs occurring mainly in the autumn and new pairs more prevalent later (Robertson *et al.* 1998). Reuniting with the same mate may confer extra advantages (Savard 1985; Black 1996). Additionally males from reunited pairs are on average older and more experienced, and probably more likely to be able to maintain a pair bond throughout the winter than younger and less experienced males (Robertson *et al.* 1998). These results suggest that although there is strong pressure for males to try to obtain a mate, the high cost of mate guarding prevents younger or less experienced males from pairing earlier.

In this study we tested some of the predictions from the male costs female benefits hypothesis of the timing of winter pairing in Harlequin Ducks. If being paired is costly for

males, we would expect that (1) paired males will show a reduction in their feeding time, and (2) paired males will display a greater frequency of interactions (courtship, mate guarding and agonistic behavior) than unpaired males. (3) If being paired is beneficial for females, we will expect that, compared to unpaired females, paired females will show an increase in their feeding time, and (4) paired females will have a lower frequency of interactions.

Because individuals may differ by more than pairing status (e.g., younger birds are generally unpaired), in a sample of marked birds for which we had information (four females with radio devices and four females with leg bands), we tested predictions 1-4 for the same individuals before and after they paired.

METHODS

Data were collected from 25 October 1996 to 7 May 1997 near White Rock, British Columbia. The numbers of Harlequin Ducks that winter in this area ranged from 75 to 150 individuals (Cooke *et al.* 1997; Robertson *et al.* 1999). Since 1994, Harlequin Ducks were each marked with a colored tarsal band engraved with a two-digit alphanumeric code and a standard United States Fish and Wildlife Service metal band.

Observations were made from a railway track, 3 m above the shoreline using 10 × 50 binoculars and a 20–60× telescope. Focal-animal sampling during 30-minute sessions were used to estimate the time budgets and the frequency of agonistic, courtship, and mate guarding behavior (hereafter referred to as interactions) (Altman 1974). Focal birds were randomly selected and sessions were distributed throughout the daylight hours as much as possible. We recorded the sex, pair status, and identity (band number or radio frequency) of the focal bird, and the date, location, and starting time of each session. Band numbers were read when the focal bird hauled-out, which is a common behavior in the Harlequin Duck. Pair status was determined by the bird's behavior before a session started. Paired birds usually remained close to each other, moved synchronously, and when a conspecific bird (hereafter referred to as the extra bird) approached, males defended their mates vigorously (Gowans *et al.* 1997). During each sample session, an observer and a writer, recorded the time (± 1 s) that the focal bird spent feeding, in maintenance activities, and the duration and frequency of interactions. When the focal bird was diving, we recorded the duration of time underwater and the surface time between dives, and whether food was brought to the surface. Maintenance activities included preening, splash-bathing, hauling-out, and resting (head-back or just drifting on the water).

The following social behavioral activities were recorded: *Rushing*, when a bird chased a conspecific, *Head-nodding*, when a bird moved his head up-down in an elliptical pattern, and *Copulation*, when the male

mounted the female and their cloacas came into contact (detailed description in Gowans *et al.* 1997). In all interactions we recorded the sex and pair status of the extra bird.

To compare variations within individuals, five males and eight females were implanted with radio transmitters (Holohil, Ltd.). The radios were implanted in late summer before pairing started, when the birds were molting. Some molting birds stayed in the same location throughout the winter, whereas others move away and winter elsewhere, returning in the following molt period (Robertson and Cooke 1999). Only four radio-marked females stayed at the study site during the period of the study, the rest of the marked birds move to different sites during the mid-winter period. All radio-marked birds were seen at the end of the wintering season, or in the following molt period.

Time budget data were analyzed using an Analysis of Covariance with sex and status as factors and date as a continuous variable (Sokal and Rohlf 1981). To account for variations through the winter in the number of daylight hours, we analyzed the estimated number of hours per day (= proportion of time spent in one activity per session * daylight hours) that the focal bird spent feeding and in maintenance activities. For the analysis of marked individuals we compared time budgets (data were arcsine transformed for the analysis to arcsine \sqrt proportion) before and after pairing by a paired t-test. In all of these analyses we verified that the residuals were normally distributed.

To compare the average dive time and surface time (time between dives) of paired and unpaired birds, data from males and females were pooled and analyzed using a Repeated Measures Design (PROC MIXED; SAS 1996). For this analysis, we included all sessions where the focal bird dove at least 15 times (341 sessions; 12,086 dives). The repeated measure was all the diving or surface times within a session. To control for variation through the season we used the residuals from a regression of dive time on season. Post-hoc comparisons were made using the Bonferroni method.

The frequency of interactions was analyzed using a Backwards stepwise Generalized Linear Model with Poisson error distribution and a log link function (Crawley 1993). In this model, the effect of a term was measured by the change in deviance, which is distributed asymptotically as 2, when that given term is removed from the maximal model (Crawley 1993). Yates' correction was used in all Chi-square tests (Sokal and Rohlf 1981). All means are presented ± 1 SD.

RESULTS

Feeding Time

The expected reduction in feeding time for paired males compared to unpaired males, and increase in feeding time for paired females compared to unpaired females were not supported by the data when the total time spent feeding was considered. Mean time spent feeding was 6.9 ± 3.0 h/day and 6.4 ± 3.6 h/day for 120 paired and 82 unpaired males, respectively ($t_{200} = 1.06$, n.s.),

and 7.8 ± 2.8 and 7.3 ± 2.9 for 119 paired and 79 unpaired females, respectively ($t_{196} = 1.23$, n.s.). Pooled data from males and females showed that the estimated number of hours spent feeding increased 16% (approximately one h) through the winter season ($F_{1, 103} = 5.00$, $P < 0.02$). The reproductive status, i.e. paired vs. unpaired, did not explain a significant proportion of the variation ($F_{1, 103} = 1.64$, n.s.). However, females spent 14% more time feeding than males ($F_{1, 103} = 10.73$, $P < 0.001$; Fig. 1a). From late October (week 2) to late April (week 28), the estimated number of hours per day spent feeding in-

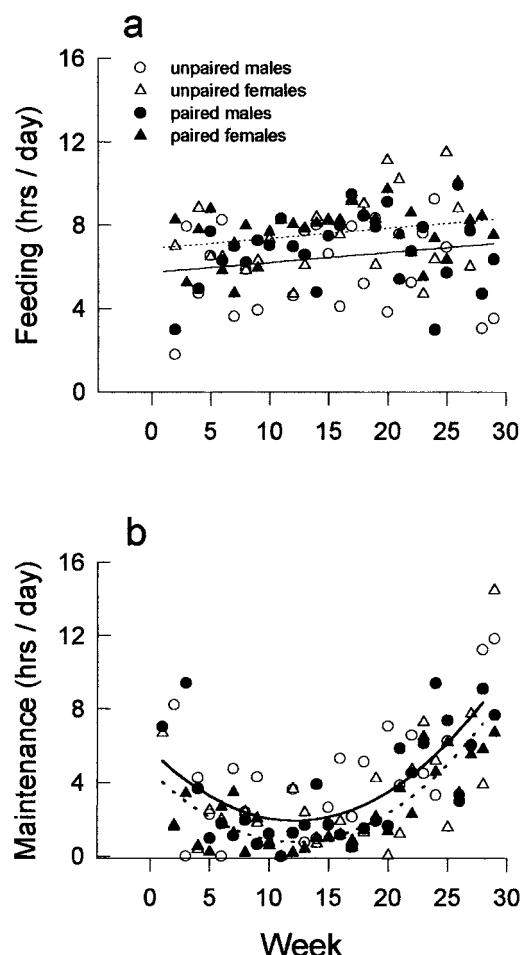


Figure 1. Time spent (a) feeding and (b) in maintenance activities by Harlequin Duck males ($N = 202$) and females ($N = 198$) according to their pair status. Week 1 = 20 October, 1996. Data were analyzed using a Generalized Linear Model. Solid lines for males and dotted lines for females.

creased from 7 to 8 h for females, and from 6 to 7 h for males (Fig. 1a).

Diving

When diving time (time underwater) was considered, our prediction was supported only for males. Paired males spent less time underwater than unpaired males. However, there was no difference in diving time between paired and unpaired females. After fitting the maximal model, pooled data of paired and unpaired males and females (341 sessions and 12,086 dives) showed that the average diving time varied with the sex and the status of the bird (Repeated Measures Model, interaction term sex*status, $F_{1,339} = 17.3$, $P < 0.001$). *Post-hoc* comparisons showed that paired males spent less time underwater than unpaired males, 22.9 ± 6.6 s ($N = 103$) vs. 23.9 ± 8.3 s ($N = 63$), respectively ($t_{164} = 5.24$, $P < 0.001$). The differences between paired and unpaired females were not significant, 23.2 ± 7.2 s ($N = 107$) vs. 23.0 ± 6.7 s ($N = 68$), respectively ($t_{173} = 0.47$, n.s.).

Males spent 16% more time on the surface between dives than females ($F_{1,337} = 24.4$, $P < 0.001$). However, the differences between paired and unpaired birds were not significant (status, $F_{1,337} = 0.03$, n.s.; sex*status, $F_{1,337} = 1.9$, n.s.). Average surface times were: 19.2 ± 30.7 s for 63 unpaired males, 18.5 ± 29.9 s for 103 paired males, 16.0 ± 22.0 s for 68 unpaired females, and 16.5 ± 32.8 s for 107 paired females.

Maintenance Behavior

The number of hours per day spent in maintenance activities changed through the winter season. Maintenance time decreased until the second week of January (week 12), and then increased until the end of the season (linear term, $F_{1,104} = 29.8$, $P < 0.001$, quadratic term, $F_{1,104} = 64.3$, $P < 0.001$; Fig. 1b). Females spent less time in maintenance activities than males throughout the winter, the estimated number of hours per day in maintenance activities were 2.5 ± 1.8 for females and 3.7 ± 1.8 for males ($F_{1,104} = 9.8$, $P < 0.01$; Fig. 1b). The differences between paired

and unpaired birds were not significant ($F_{1,104} = 2.0$, n.s.; all interaction terms were not significant).

Interactions

Paired males performed a greater frequency of interactions than unpaired males. The mean frequency of interactions per 30-min. session was 2.0 ± 1.3 for paired males and 0.6 ± 0.8 for unpaired males ($\chi^2_1 = 81.0$, $P < 0.001$). The estimated frequency of interactions decreased 38% through the winter season, however, variations through the winter were not significantly different for paired and unpaired males (date, $\chi^2_1 = 5.2$, $P < 0.02$; date*status, $\chi^2_1 = 0.8$, n.s.; Fig. 2a).

Most of the interactions recorded were male-male (focal bird-extra bird): 68% (166/244) for paired males, and 61% (30/49) for unpaired males (Table 1). A greater proportion of the male-male interactions were performed with extra-unpaired males compared to extra-paired males ($\chi^2_1 = 8.8$, $P < 0.01$; Table 1). However, the pair status of the focal bird was not significant, the proportion of interactions with extra unpaired males was 43% (106/244) for paired males and 45% (22/49) for unpaired males ($\chi^2_1 = 0.001$, n.s.; Table 1).

The proportion of interactions with females was different among paired and unpaired males. Paired males interacted less frequently with unpaired females than did unpaired males: 5% (13/244) vs. 39% (19/49), respectively ($\chi^2_1 = 43.5$, $P < 0.001$; Table 1). When interacting with females, paired males did so more frequently with their mates, 98% of the 65 interactions with paired females were with their mates (Table 1). In contrast, there were no direct interactions by unpaired males towards a paired female (Table 1).

Interactions for focal females were classified according to whether the focal female received or performed the interaction. Overall, paired and unpaired females received a similar frequency of interactions per session, 0.73 ± 1.5 and 0.79 ± 1.7 respectively ($\chi^2_1 = 0.5$, n.s.). However, paired females showed a decrease from 1.7 interactions in late Octo-

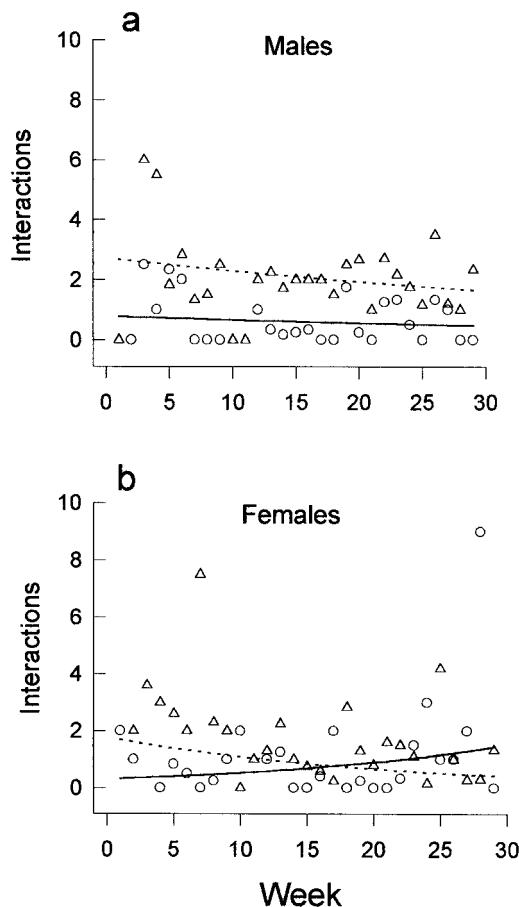


Figure 2. Frequency of interactions (a) performed by focal males, and (b) received by focal females. Symbols are circles for unpaired birds, and triangles for paired birds. Week 1 = 20 October, 1996. Data were analyzed using a Generalized Linear Model with a Poisson error distribution. Solid lines for unpaired birds and dotted lines for paired birds.

ber to 0.4 by early May, while the interactions received by unpaired females increased from 0.3 to 1.4 for the same period ($\chi^2_1 = 18.4$, $P < 0.001$; Fig. 2b).

Most interactions experienced by females were initiated by males: 99% (94/95)

for paired females and 90% (52/58) for unpaired females (Table 2a). Compared to unpaired females, paired females received a larger proportion of interactions from paired males: 9% (5/58) vs. 70% (66/95), respectively ($\chi^2_1 = 51.2$, $P < 0.001$; Table 2a). In contrast, interactions with unpaired males were more frequently by unpaired females than by paired females: 81% (47/58) vs. 29% (28/95), respectively ($\chi^2_1 = 36.2$, $P < 0.001$; Table 2a). Female-female interactions were uncommon (Table 2a).

Paired females initiated interactions more frequently than unpaired females ($\chi^2_1 = 5.1$, $P < 0.05$; Table 2b). Paired and unpaired females directed a similar proportion of interactions to unpaired males: 87% (28/32) vs. 70% (7/10), respectively ($\chi^2_1 = 0.01$, n.s.). Paired females also interacted with unpaired females, 6% (2/32), and paired males, 6% (2/32). Unpaired females directed 30% (3/10) of their interactions towards unpaired females.

Marked Individuals

Time spent feeding, in maintenance activities and in interactions did not differ for eight females (four radio-marked birds and four banded birds) for which we had information before and after pairing occurred. The proportion of time spent feeding was on average 0.5 (± 0.3) for unpaired females, and 0.5 (± 0.2) for paired females (paired t -test, $t_7 = 0.05$, n.s.). The proportion of time spent in maintenance activities was 0.4 (± 0.3) for unpaired females, and 0.4 (± 0.2) for paired females (paired t -test, $t_7 = 0.79$, n.s.).

As expected, females spent a smaller proportion of time in interactions after they had paired compared to before pairing, but the difference was not significant. The propor-

Table 1. Male behavioral interactions according to their own and to the extra bird's reproductive status (paired/unpaired) in the Harlequin Duck.

Focal bird	Extra bird				Total
	Unpaired male	Paired male	Unpaired female	Paired female	
Unpaired	22	8	19	0	49
Paired	106	60	13	65	244

Table 2. Female behavioral interactions according to their own and to the extra bird's reproductive status (paired/unpaired) in the Harlequin Duck. Interactions were divided according to whether the focal female (a) received or (b) performed the interaction.

Focal bird	Extra bird					Total
	Unpaired male	Paired male	Unpaired female	Paired female		
a. Focal female received the interaction						
Unpaired	47	5	3	3	58	
Paired	28	66	0	1	95	
b. Focal female performed the interaction						
Unpaired	7	0	3	0	10	
Paired	28	2	2	0	32	

tion of time spent in interactions was on average 0.02 (± 0.02) for paired females, and 0.08 (± 0.12) for unpaired females (paired t -test, $t_7 = 0.96$, n.s.).

DISCUSSION

In terms of foraging behavior our predictions were partially supported. Maintaining a pair bond incurred some costs to males but we found no evident benefit for females. Paired males spent less time underwater than unpaired males, although pair status did not affect the diving behavior of females, nor did pair status affect the total time that males and females spent foraging.

The reduction in the male's time underwater probably resulted from his behavior once paired. When diving, pairs do so in a synchronous fashion. Typically, the female submerges first and the male follows, diving almost in the same spot as the female but one to two seconds later. This is especially obvious when an extra male is nearby. Synchronous diving of pairs may be a way of pair-bond maintenance and mate guarding. This delay made by males before diving may be part of the mate guarding strategy in this species. However, by submerging after the female, males lost time underwater and may have reduced the probability of capturing food. During the winter, preferred food items of Harlequin Ducks include mobile prey like small crabs, amphipods, isopods and fish (Vermeer 1983; Goudie and Ankney 1986).

Overall, and independently of pair status, females spent more time feeding than males.

There are different possible nonexclusive explanations of why females invest more time feeding. Based on mass-specific differences in metabolic rates, it is expected that in species with sexual size dimorphism, individuals of the smaller sex will consume more food relative to their body size (Calder 1974). [Smaller individuals have the thermodynamic disadvantage of accelerating the rate of body heat loss, increasing their food requirements relative to their body size (Calder 1974).] Also, females may increase the time spent feeding to be able to build body reserves to breed (e.g., Ankney and MacInnes 1978). If this were true for the Harlequin Duck, we would expect that the difference in the time spent feeding between males and females to be greater, and that females, but not males, would show an abrupt increase a few weeks before migration. In fact, we recorded a gradual and proportional seasonal increase in feeding time, which could result from changes in food availability. Also, more recent studies suggest that Harlequin Duck females may not be accumulating body reserves during the winter to prepare for breeding. In a northern group of Harlequin Ducks, Fischer (1998) reported a decline in mass and body fat over the winter in females, while males showed a peak in mid-winter. It is possible that females gather most of the reserves they use for breeding during the four to six weeks they spent on the pre-breeding sites on the rivers before egg laying; at these sites females spent more time feeding than males (Hunt 1998; Robertson and Goudie 1999). In our study, we were unable to record

feeding success underwater, thus, we cannot reject the possibility of greater foraging efficiency in males than in females.

The prediction that paired males perform a greater frequency of interactions than unpaired males was supported by the data. Because the sex ratio is biased towards males in this group, male-male competition is intense (Gowans *et al.* 1997; Robertson *et al.* 2000). In our study, when the focal bird was a paired male, most interactions were with an extra male. In all cases, the focal male would counter the approach of a conspecific, keeping him away from his mate, or even expelling him from the area. Paired males were successful in keeping unpaired males away from their mates. When the focal bird was an unpaired male we did not record any interactions with a paired female (Table 1). Male Harlequin Ducks do not form territories in winter and the behavioral interaction was a result of mate guarding by the male (Gowans *et al.* 1997; Robertson *et al.* 2000).

Females received more interactions from males of a similar status to themselves. For paired females, most of these interactions were from their own mate. Interactions initiated by focal females were less frequent and often directed towards unpaired males, in most cases to chase them away. Thus, although it was not frequently observed, paired females can aggressively keep away extra males and females.

The frequency of interactions for males and females changed over the season, probably as a result of seasonal changes in the sex ratio. As more pairs were established, the bias among unpaired birds towards males increased (Robertson *et al.* 1998; Robertson *et al.* 2000). Throughout the season, the probability of interacting was three times greater for paired than for unpaired males. As the season progressed, the probability of interactions occurring decreased for paired females and increased for unpaired females. This, probably reflected the fact that in the early part of the winter reuniting pairs are active, and these females are scored as paired, whereas in the later part of the winter, unpaired females are under increasing pressure from the many unpaired males.

Differences among individuals (e.g., age, or reproductive experience) may account for some of the variation in the time budgets and behavioral interactions we recorded. To further evaluate the costs and benefits of being paired, comparisons before and after the pair bond was established for the same marked individuals were carried out. We did not find differences before and after these birds formed pair bonds. However, the sample sizes of individually marked birds were small.

Our results showed that winter pairing might be costly for males (increased investment in social interactions and slight reduction in time underwater), although the benefits for females were not so clear. Paired females showed a seasonal decrease in the frequency of interactions with conspecifics, yet female feeding time, and presumably the ability to acquire nutrients, did not increase. Thus, other factors may be important to explain the timing of pairing in the Harlequin Duck.

When there is a strong advantage to have the same mate as in the previous year, both males and females should favor early pairing. The Harlequin Duck breeds with the same partner during consecutive seasons (Robertson *et al.* 1998). Pair reunion occurred in the autumn, whereas most new pair bonds (mainly yearlings and sub-adults) were established in spring (Robertson *et al.* 1998). Mating with the same partner should enhance reproductive success by reducing the costs of mate sampling, and by improving co-ordination and cooperation with a mate (Black 1996), and this advantage may be much greater than the costs associated with a reduction in feeding time. For new pairs, timing of pairing is probably more variable, and strongly determined by female choice. Because of the male-biased sex ratio and high probability of completely failing to obtain a mate, males may be more ready to pair earlier than females. Females need to balance the advantages of a wider choice of potential mates early in the winter with the advantages of assessing the available males for suitability over a longer time period. Although our data are not totally contrary to Rohwer and Anderson's hypothesis, they do not support

the prediction of increased feeding time for females. An alternative explanation is that, in the Harlequin Duck, the benefit of early pairing for females is not in terms of increasing feeding time, but rather early pairing in this species may be favored by the advantages of pair reunion.

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LITERATURE CITED

- Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. *Auk* 101: 255-265.
- Altman, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49: 227-267.
- Ankney, C. D. and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser snow geese. *Auk* 95: 459-471.
- Bengtson, S. A. 1972. Breeding ecology of the Harlequin Duck *Histrionicus histrionicus* in Iceland. *Oikos* 3: 1-19.
- Black, J. M. 1996. Partnerships in birds: the study of monogamy. Oxford Ornithology Series, Oxford University Press.
- Brodsky, L. M. and P. J. Weatherhead. 1985. Time and energy constraints on courtship in wintering American Black Ducks. *Condor* 87: 33-36.
- Calder, W. A. III. 1974. Consequences of body size for avian energetics. Pages 86-151 in Avian energetics Nutall Ornithol (R. A. Paynter, Ed.). Cambridge, MA.
- Cooke, F., G. J. Robertson, I. R. Goudie and W. S. Boyd. 1997. Molt and the basic plumage of male Harlequin Ducks. *Condor* 99: 83-90.
- Crawley, M. 1993. GLIM for Ecologist. Blackwell Scientific Publications. Oxford.
- Fischer, J. B. 1998. Feeding behaviour, body condition, and oil contamination of wintering Harlequin Ducks (*Histrionicus histrionicus*) at Shemya Island, Alaska. Unpublished MSc thesis, Univ. of Massachusetts, Amherst.
- Goudie, R. I. and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67: 1475-1482.
- Gowans, B., G. J. Robertson and F. Cooke. 1997. Behaviour and chronology of pair formation by Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl* 48: 135-146.
- Hepp, G. R. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. *Auk* 103: 477-484.
- Holmberg, K., Edsman, L. and K. Thorsten. 1989. Female mate preference and male attributes in mallard ducks *Anas platyrhynchos*. *Animal Behaviour* 38: 1-7.
- Hunt, W. A. 1998. The ecology of Harlequin Ducks (*Histrionicus histrionicus*) breeding in Jasper National Park, Canada. Unpublished MSc. Thesis Simon Fraser University, Burnaby, BC. Canada.
- McKinney, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pages 153-171 in Ecological aspects of social evolution (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton University Press, Princeton.
- Owen, M. and M. Dix. 1986. Sex ratios in some common British wintering ducks. *Wildfowl* 37: 104-112.
- Paulus, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100: 947-952.
- Robertson, G. J., F. Cooke, R. I. Goudie and W. S. Boyd. 1998. The timing of pair formation in Harlequin Ducks. *Condor* 100: 551-555.
- Robertson, G. J., F. Cooke, R. I. Goudie and W. S. Boyd. 1999. Within-year fidelity of Harlequin Ducks to a molting and wintering area. Pages 45-51 in Behaviour and ecology of seabirds. Canadian Wildlife Service Occasional Paper Series No. 100 (R. I. Goudie, M. R. Petersen and G. J. Robertson, Eds.). Ottawa, Ontario.
- Robertson, G. J. and F. Cooke. 1999. Winter philopatry in migratory waterfowl. *Auk* 116: 20-34.
- Robertson, G. J. and R. I. Goudie. 1999. Harlequin Ducks, *Histrionicus histrionicus*. In: Birds of North America. Birds of North America Inc. (A. Poole and F. Gill, Eds.), Philadelphia.
- Robertson, G. J., F. Cooke, R. I. Goudie and W. S. Boyd. 2000. Spacing patterns, mating systems and winter philopatry in Harlequin Ducks. *Auk* 117: 299-307.
- Rohwer, F. C. and M. G. Anderson. 1988. Female biased philopatry, monogamy, and the timing of pairing in migratory waterfowl. Pages 187-221 in Current Ornithology Vol. 5 (D. M. Power, Ed.). Plenum Press, New York.
- SAS Institute, Inc. 1996. SAS/STAT software: changes and enhancements through release 6.11. SAS Institute, Inc., Cary.
- Savard, J. P. L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (*Bucephala islandica*). *Auk* 102: 389-391.
- Smith, C. M., Cooke, F., Robertson, G. J., Goudie, R. I. and W. S. Boyd. 2000. Long-term pair bonds in Harlequin Ducks. *Condor* 102: 201-205.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry* 2nd ed. W.H. Freeman & Company. New York.
- Spurr, E. and H. Milne. 1976. Adaptive significance of autumn pair formation in the Common Eider *Somateria mollissima* (L.). *Ornis Scandinavica* 7: 85-89.
- Vermeer, K. 1983. Diet of the Harlequin Duck in the Strait of Georgia, British Columbia. *Murrelet* 64: 54-57.