

Pairing Decisions in the Harlequin Duck: Costs and Benefits

ROXANA TORRES¹, FRED COOKE, GREGORY J. ROBERTSON² AND W. SEAN BOYD³

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

¹Present address: Departamento de Ecología Evolutiva, Instituto de Ecología
Universidad Nacional Autónoma de México, Apartado Postal 70-275, México D.F. 4510, México
Internet: ltorres@servidor.unam.mx

²Present address: Canadian Wildlife Service, 6 Bruce Street, Mount Pearl, Newfoundland A1N 4T3, Canada

³Pacific Wildlife Research Center, Canadian Wildlife Service

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 (*A. a. a. - b. b. b.*) 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 (*A. a. a. a. - c. c. c.*) 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 (*H. t. t. c. - d. d. d.*) 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: *R* (when a bird chased a conspecific, *H a* (when a bird moved his head up-down in an elliptical pattern, and *C* (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 $\sqrt{\text{proportion}}$) 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. *P*-value 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 χ^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-

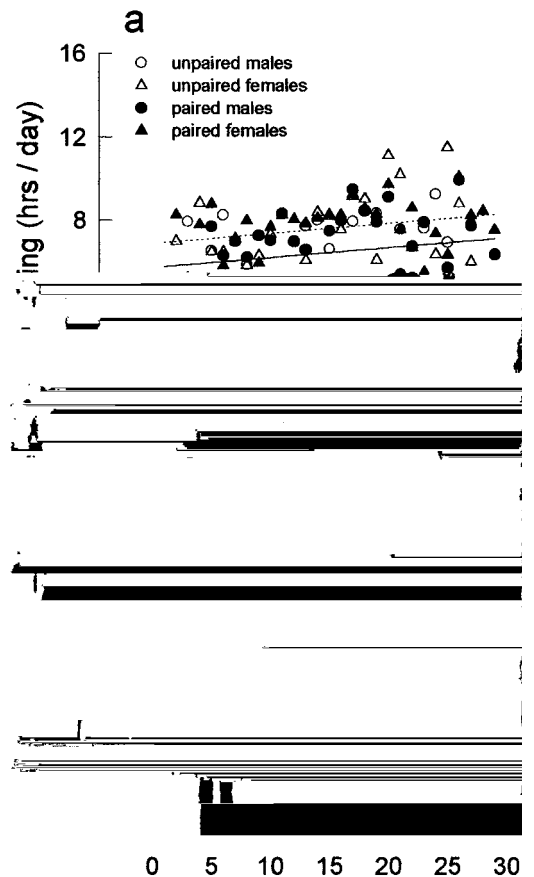


Figure 1. Time spent (a) feeding and (b) in maintenance activities by Harlequin Duck males (N = 202) and females (N = 198) according to their pair status. Week 1 = 20 October, 1996. Data were analyzed using a Generalized Linear Model. Solid lines for males and dotted lines for females.

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 un-

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

