Timing of Pairing in Waterfowl II:
Testing the Hypotheses with Harlequin Ducks

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Abstract.—Intra-specific predictions of the male-costs and mutual-choice hypotheses to explain variation in the timing of pairing in waterfowl were tested in a longitudinal study of marked, known-aged Harlequin Ducks (*Histrionicus histrionicus*). Pairing chronologies and seasonal changes in time-activity budgets and rates of aggressive interactions were compared in relation to sex, age, and paired status. Results supported the mutual-choice and not the male-costs hypothesis. Paired females gained no immediate benefits relative to unpaired females from mate defense and vigilance, and there was no evidence that females preferred to pair as early as possible, as postulated by the male-costs hypothesis. Unpaired males spent much more time in courtship than paired males spent in mate defense and constraints on male time and energy budgets was not a plausible reason for delayed and protracted pairing of young and re-pairing females. As predicted by the mutual-choice hypothesis, decisions by females about how much time and energy to allocate to the pairing process appeared to be the main factor controlling the timing of pairing in Harlequin Ducks. Newly-pairing females invested an extended period of time in courtship and mate sampling before pairing, in spite of an abundance of courting males clearly energetically capable of maintaining a pair bond. Many young females decided to pair during mid-winter when time constraints to males should have been most severe. Time-budget trade-offs were apparent for young females and their date of pairing was related to the amount of time per day that they allocated to courtship. Pairing success of males was not related to their rate of courtship, nor was it related to the length of time they invested in courtship as they began courting while they were still immature and generally courted for several years before pairing. *Received 15 November 2006, accepted 1 June 2007.*

Key words.—Cost-benefit trade-offs, courtship, female mate choice, Harlequin Duck, *Histrionicus histrionicus*, pairing chronology, sexual selection, winter time budgets.

Many waterfowl species form pair bonds months or even years before breeding, in contrast to the more common avian pattern of pairing just prior to reproduction (Lack 1968). Some species of other avian families (e.g., penguins, corvids, parids) also pair far in advance of breeding, but the behavior has received most attention in waterfowl and a variety of hypotheses have been generated to explain it (reviewed in Rohwer and Anderson 1988; Oring and Sayler 1992). The main hypothesis in use to explain variation in the timing of pairing in waterfowl suggests that early pairing benefits females (through increased foraging efficiency and survival due to male defense and vigilance) and males (through mate acquisition and improved female condition) but is constrained by costs to males of courtship, mate defense, and vigilance which may tip the cost-benefit balance of maintaining a pair bond to favor later pairing (*male-costs hypothesis*; Rohwer and Anderson 1988; Owen and Black 1990; Or-

ing and Sayler 1992). A review of available data found little support for this hypothesis and considerable data that were inconsistent with its predictions (Rodway 2007; Table 1).

The male-costs hypothesis is incomplete because it fails to consider cost-benefit trade-offs to females and the relevance of female mate choice, and, for both sexes, ignores trade-offs among three components of the pairing process: the process of choosing a mate, the quality of mate chosen, and the state of being paired, including potential benefits of time spent gaining familiarity with a partner before breeding. The *mutual-choice hypothesis* extends the male-costs hypothesis by considering cost-benefit trade-offs to both females and males, and suggests that individuals will decide to pair when the combined fitness benefits of the different components of the pairing process are maximized (Rodway 2007). Inter- and intra-specific variation in the timing of pairing then results from variation in the costs and bene-

fits of the three components due to differences in reproductive tactics, differences by sex, age, and pairing experience, and differing social and ecological conditions. In most waterfowl, decisions by females rather than males will primarily determine the timing of pairing. Many available data were consistent with predictions of this hypothesis (Table 1), but adequate testing of the hypothesis was hampered by a lack of data on age- and sex-specific pairing chronologies and associated measures of individual behavior and time-activity budgets (Rodway 2007).

Objectives of this study were: 1) to test intra-specific predictions of the male-costs and mutual-choice hypotheses by conducting a longitudinal study of marked, known-aged Harlequin Ducks (*Histrionicus histrionicus*), and 2) to provide a detailed picture of time-activity budgets and social interactions of paired and unpaired individuals of this species that will help refine hypotheses and contribute to our understanding of pairing behavior in waterfowl. A number of predictions of the two hypotheses were derived in Rodway (2007) and are summarized in Table 1. Here those predictions are tested by comparing pairing chronologies by sex, age, and previous pairing history, and by comparing seasonal changes in time-activity budgets and rate of aggressive interactions in relation to sex, age, and paired status.

Harlequin Ducks have a monogamous mating system with no paternal care and male desertion during incubation. They form multi-year pair bonds on the wintering grounds (Gowans *et al.* 1997; Smith *et al.* 2000) and there are age-specific differences in the timing of pairing (Robertson *et al.* 1998). Feeding takes a large proportion of their time during winter months (Goudie and Ankney 1986; Torres *et al.* 2002), except when birds are feeding on Pacific herring (*Clupea pallasi*) spawn (Rodway 2006) that is available for three-to-four weeks in March-April (Rodway and Cooke 2002; Rodway *et al.* 2003b). This change in food availability and associated changes in time-activity budgets and behavior of pairing birds provided an opportunity to test certain predictions of the male-costs and mutual-choice hypotheses.

STUDY AREA AND METHODS

Marking and Aging

About 3,500 Harlequin Ducks have been marked in the Strait of Georgia in 1993-2000 as part of a joint effort between Canadian Wildlife Service and Simon Fraser University (details in Robertson *et al.* 1998; Rodway *et al.* 2003b). Since 1994, all captured birds have been marked with unique, alpha-numeric colored leg bands. Captured birds were sexed and aged by plumage, cloacal examination, and the depth of the Bursa of Fabricius (Kortright 1942), except for first-year males that could be identified throughout the winter by their Alternate I plumage (Smith *et al.* 1998). Four age classes were discriminated: first (1Y), second (2Y), and third year (3Y), and after third year (A3Y; Smith *et al.* 1998; Mather and Esler 1999). Birds were considered 1Y, 2Y, and 3Y throughout their first, second, and third winters, respectively, and A3Y afterwards.

Unique, shape-color-combination nasal discs were put on 457 birds, most in 1998-99, plus a few in 1997 and 2000. Nasal discs decreased pairing success of males and increased mate change in previously paired females but did not affect timing of pairing or other behaviors (Regehr and Rodway 2003). Thus, all marked birds were used to determine pairing chronology. Effects of nasal discs on males would not affect pairing success of females because sex ratios are male biased 1.5:1 (Rodway *et al.* 2003a).

Pairing Chronology

Pairing chronology was assessed using four of the five measures recommended by Rodway (2007): 1) court-age (the age at which young individuals first begin courtship), 2) court-time (the number of days or months that newly-pairing or re-pairing individuals are engaged in courtship activity and mate sampling, including trial liaisons, before pairing), 3) court-rate (the amount of time per day allocated to courtship), and 4) pair-date (the calendar date that pairing occurs). Pair status was judged based on observed behavior (Gowans *et al.* 1997). Pair status was considered confirmed for an individual if it behaved paired or unpaired for most of an observation session of 30 min or more, or if it appeared consistently paired or unpaired at least twice when it was observed for shorter periods of time. An exception was made for birds re-uniting with a known mate; only one observation of being paired was required in that case. For birds that were confirmed paired, the timing of pair formation (pair-date) was taken as the first date on which they were observed paired, unless subsequent data confirmed that initial pairing was a temporary liaison. Individuals were included in the sample used to determine pairing chronology if they paired before November, or, if they paired later, only if they were observed not paired no more than 30 d prior to when they were first observed paired. This method ensured that estimates of pair-date were not biased by birds that were first seen paired later in the winter but could have paired much earlier. All birds pairing before November were included because females are completing their post-breeding molt during September and October (Robertson *et al.* 1997), few initiate pairing until October (Gowans *et al.* 1997; Robertson *et al.* 1998), and many of those pairing in late September and October were not observed prior to when they were first seen paired. Estimates for pair-date are thus considered accurate within 30 d for all birds.

Table 1. Predictions of the *male costs* and the *mutual-choice* hypotheses to explain variation in the timing of pairing in waterfowl, as measured by the date of pairing (pair-date), the number of days spent in courtship and mate-sampling (court-time), and the amount of time allocated to courtship per day (court-rate), and in relation to time-activity budgets during the non-breeding season. Predictions were derived in Rodway (2007). Herring spawn is available to Harlequin Ducks in March.

Male-costs predictions	Mutual-choice predictions	Available data (*in litt.*)[a]	Harlequin Ducks (this study)
Pairing chronology: intra-specific trends			
Pair-date			
Young females pair at same time or earlier than older females when sex ratios are male-biased	Young females pair later than previously paired females; re-uniting females pair earliest	Young females later even when sex ratios are male-biased	Young females pair later; re-uniting females pair earliest
All unpaired females pair as soon as herring spawn is available	Pairing occurs at accelerated rate through and after spawn period	No data	Young females pair through and after spawn period
Young males pair later than older males	Young males pair later than older males	Young males pair later	Young males pair later
Court-time			
No necessary trend	Court-time greater for naive than experienced birds	No data	Court-time greater for naïve birds
Court-rate			
No trend for females	Female pair-date earlier with higher court-rate	No data	Female pair-date earlier with higher court-rate
Male pairing success greater and pair-date earlier with higher court-rate	No necessary trend	No data	No trend for males
Winter time-activity budgets			
Feeding			
Paired females spend more time feeding than unpaired females	No necessary trend	No difference	No difference except unpaired more during herring spawning
Unpaired males spend more time feeding than paired males	No necessary trend	No difference	Unpaired less through winter; more during herring spawning
Courtship			
Unpaired males spend less time in courtship than paired males spend in mate defense	Unpaired males spend as much or more time in courtship than paired males spend in mate defense	Unpaired spend more time in courtship than paired spend in defense	Unpaired males spend more time in courtship than paired males spend in defense
No necessary trend	Unpaired birds increase court-rate when herring spawn available	No data	Unpaired birds increase court-rate when spawn available
Aggressive interactions			
Paired females receive less than unpaired females	No necessary trend	No difference	Less for paired females but no difference outside courtship
Vigilance			
Paired females spend less time than unpaired females	No necessary trend	No difference	No difference

[a]See Rodway (2007) for references.

Proportions of various sex- and age-classes paired at the end of winter were determined using the same criteria listed above for confirming pair status but including only observations made in March, April, and May. Even so, some birds called unpaired may still have paired that spring and estimates of proportion paired are conservative. Individual pair-dates, determined as described above, and the total proportion paired at the end of the winter, were used to estimate the relationship between proportion paired and date for each age-sex class. Proportions of known-aged birds identified as paired during each month were also used to corroborate observed patterns. In that case, the criteria for confirming paired status was relaxed to obtain adequate sample sizes, accepting one or more consistent observations of pair status per individual. Requiring only one observation made it more likely that errors were made in assigning pair status, but within a month biases towards more

paired or more unpaired birds were unlikely, especially because pair status was typically quite obvious.

Behavioral Observations

Continuous observations of focal birds (Altmann 1974) were conducted throughout daylight hours. Most observation sessions were five min, but sessions in 1998 and some in 1999 were 30 min. Duration to the nearest second of feeding, moving, preening, resting, courtship, vigilant, and aggressive (including mate-guarding) behaviors and the frequency of agonistic interactions (Inglis *et al.* 1989) were recorded during each session. Both the proportion of diurnal time and the absolute amount of time per day spent in each behavior are presented, because proportion of time best indicates time constraints relative to time required for feeding, while absolute amount of time best indicates seasonal changes in total time spent in each activity. Absolute amount of time spent in different behaviors was calculated by multiplying proportions of time spent in those behaviors during observation sessions by the estimated number of daylight hours that birds were present in nearshore habitat. Time present nearshore was calculated as the time between sunrise and sunset (U.S. Navy 2000) adjusted by the median arrival or departure times relative to sunrise or sunset determined by Rodway and Cooke (2001) for each relevant date category.

Analyses

Kruskal-Wallis and Mann-Whitney U-tests were used to compare pairing chronologies among different classes of birds. Proportional data were arcsine transformed to satisfy assumptions for parametric tests. Variation in activity budgets was analyzed using full factorial ANOVA. Interaction terms were dropped from final models if they were not significant. Data were initially categorized into two location categories, areas where herring did and did not spawn, and seven date categories, October, November, December, January, February through to the beginning of herring spawning in early March each year (February), the three-week period in March after herring spawning began each year (March), and from the end of the spawning period through April (April). Preliminary analyses indicated no consistent differences among locations except during herring spawning, and

thus a single date-location variable was used with eight categories: October, November, December, January, February, March without spawning, March with spawning, and April. The date-location variable was included in all analyses comparing time budgets among different classes of birds to control for differences due to date and the availability of herring spawn. Sex and paired status were combined into a single variable (sex-pair). Unadjusted means ± SE are reported for date-location categories, and adjusted means from a 2-way ANOVA including date-location are reported for sex-pair classes.

RESULTS

Pairing Chronology

There was good agreement between the two measures of pair-date (Table 2, Fig. 1) except when monthly sample sizes per age class were too small to adequately assess proportions paired (Table 2). Some females formed initial pair bonds in the spring of their first year and almost all paired in their second year. About 40% of 2Y females paired during mid-winter from November to February and 50% paired in March and April. Older females paired earlier than younger females (Kruskal-Wallis $H_3 = 35.4$, $P < 0.001$; all pairwise comparisons: $P < 0.05$ with Bonferroni corrections). No males were observed paired in their first year (N = 109), a few began pairing in March of their second year, but the majority did not pair until they were > three y old. Most females > two y old and most males > three y old paired in October and November.

Mean (± SD) pair dates of A3Y females (17 Oct ± 12 d, N = 39) that were re-uniting with former mates were earlier than pair

Table 2. Monthly changes in the percentage (n) of marked, first-, second-, third-, and after-third-year female and male Harlequin Ducks that were identified as paired in the Strait of Georgia, British Columbia, 1995-2001. Percentages within each month are based on the number of birds whose apparent pair status was determined one or more times in that month.

| Month	Female age				Male age		
	1	2	3	>3	2	3	>3
Sept	0.0 (1)	0.0 (13)	0.0 (14)	2.0 (100)	0.0 (1)	0.0 (7)	1.8 (113)
Oct	0.0 (1)	9.1 (11)	20.0 (20)	51.9 (131)	0.0 (1)	9.1 (11)	39.3 (112)
Nov	0.0 (4)	5.3 (19)	55.6 (18)	77.4 (133)	0.0 (4)	9.1 (11)	54.2 (120)
Dec	0.0 (0)	0.0 (1)	61.5 (13)	98.0 (49)	0.0 (1)	0.0 (4)	52.4 (42)
Jan	0.0 (2)	41.7 (24)	82.1 (28)	94.4 (108)	0.0 (2)	14.3 (7)	51.8 (85)
Feb	0.0 (5)	43.8 (16)	90.0 (20)	92.5 (120)	0.0 (3)	20.0 (10)	59.4 (101)
Mar	20.0 (10)	81.8 (55)	90.6 (64)	96.9 (451)	19.0 (21)	18.2 (33)	65.0 (592)
Apr	33.3 (3)	95.2 (21)	100.0 (36)	99.4 (159)	28.6 (7)	44.4 (9)	75.9 (191)
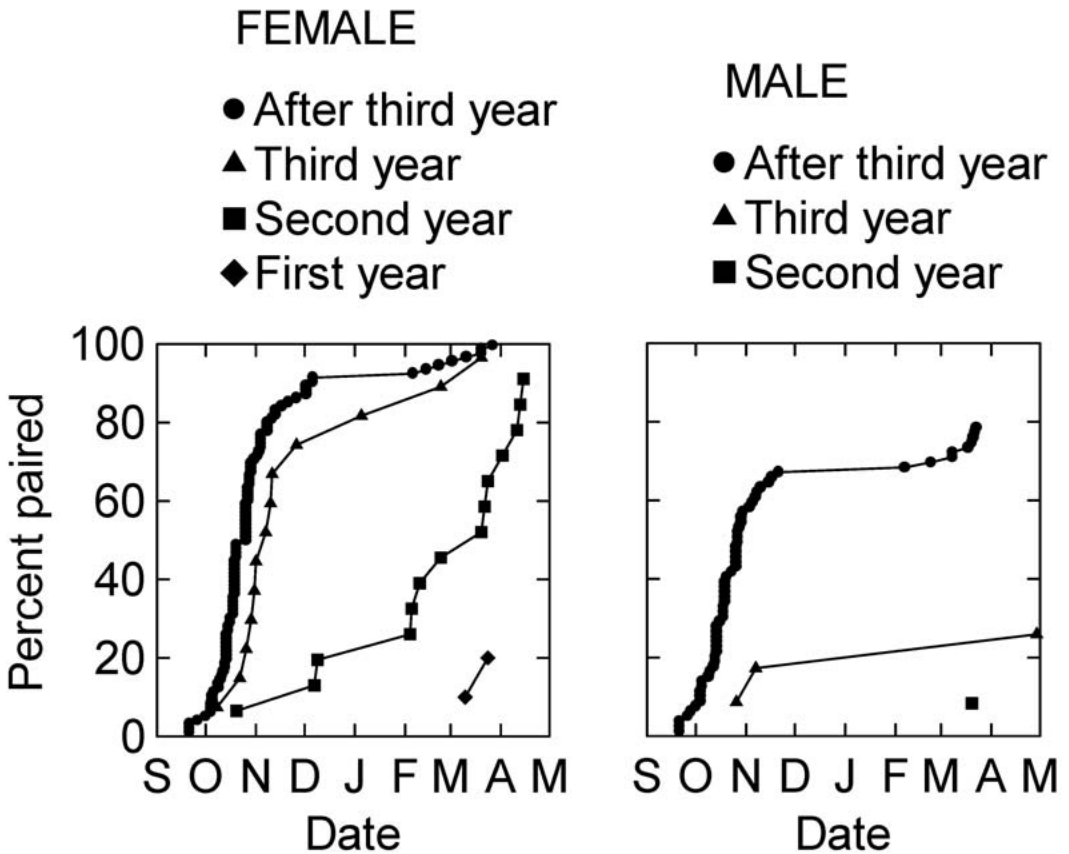
Figure 1. Age-related pairing chronology of Harlequin Ducks in the Strait of Georgia, British Columbia, 1995-2001. Each point represents the estimated date of pairing of a marked individual and is considered accurate within 30 d. Total percentages of each age class that paired were determined in spring out of samples of ten, 45, 58, and 367 first-, second-, third-, and after-third-year females, respectively, and three, eight, and 309 second-, third-, and after-third-year males, respectively.

dates of A3Y females (16 Nov ± 47 d, N = 57) and 3Y females (26 Nov ± 50 d, N = 13) that were re-pairing, and of 2Y females (19 Feb ± 57 d, N = 13) that were pairing for the first time (Kruskal-Wallis H_3 = 35.4, P < 0.001; pairwise comparisons: P_s < 0.003). Mean pair dates of A3Y males (17 Oct ± 14 d, N = 32) that were re-uniting with former mates were also earlier than pair dates of re-pairing A3Y males (3 Dec ± 66 d, N = 30; H_1 = 9.8, P = 0.002). Estimated differences between re-uniting and re-pairing birds are likely conservative because the re-pairing category may have included re-uniting birds whose mates were not marked or that were not observed previously as well as known re-pairing birds. Also, there was evidence that some established pairs re-unite, at least briefly, be-

fore molt has been completed. One known pair, last seen together on their wintering ground in April, were seen acting paired again on 26 July. At this time the male was in basic plumage and was flightless, and the female had just returned to the coast and had not yet initiated molt. After this brief rejoining, these birds remained in the same general area but behaved unpaired until 14 October, after which they behaved paired for the rest of that winter.

For A1Y birds, the frequency (but not rate, see below) of engaging in courtship by unpaired birds remained similar throughout the winter. No differences were found in the proportion of observation sessions during which an unpaired individual engaged in some courtship among unpaired 2Y (32%, N = 71),

3Y (34%, N = 47), and A3Y (45%, N = 67) females (G_2 = 2.5, P = 0.3) and unpaired 2Y (65%, N = 17), 3Y (54%, N = 46), and A3Y (52%, N = 208) males (G_2 = 2.2, P = 0.3), or among the months October-April for unpaired females (G_6 = 3.0, P = 0.8) and unpaired males (G_6 = 4.6, P = 0.6). Earliest observations of 1Y females being courted were in March. Three of 7 1Y females observed in March were being courted and it is likely that a majority were courted at that time because observations of specific individuals were infrequent. Frequency of courtship by 1Y males increased through the winter and, while 1Y males comprised about 9% of all males (Rodway et al. 2003a), they comprised 1.3% (N = 468), 1.7% (N = 595), 4.8% (N = 207), 4.5% (N = 374), and 4.5% (N = 161) of all males observed courting during October-November, December-January, February, March, and April, respectively (G_4 = 14.5, P = 0.006). Whether differences by date were due to increasing frequency of courtship by all 1Y males or by increasing proportions of 1Y males engaging in courtship could not be determined.

Four 1Y females appeared paired during extended observations conducted between 1 March and 4 May, and subsequently were seen unpaired. The two other 1Y females that were identified as paired (Figure 1) also likely were engaged in trial liaisons because all 2Y females observed early in the fall were unpaired (Table 2). If so, then 55% of 1Y females for which pair status was known (N = 11) were observed in temporary liaisons. Five 2Y females (13%; N = 38) were observed in trial liaisons with one or more males between 21 November and 23 January. No temporary liaisons by older (A2Y) females were detected. Of five marked males observed in trial liaisons, four did not pair again within the same year, suggesting that females and not males were responsible for temporary liaisons. Rates of trial liaisons by young females were likely underestimated because observations per individual were infrequent.

Time taken to re-pair after the disappearance of a previous mate could be determined only for a few birds. Two A3Y females re-paired twelve and 20 d after their previous mate disappeared in March, and two other

A3Y females were known to remain unpaired for three and five months during the early part of winter. A3Y males that were successful in forming another pair bond averaged ten months (range: four to 14 mo, N = 6) to re-pair, others were known to remain unpaired for at least four months (N = 1), six months (N = 2), two years (N = 1), and four years (N = 1) after losing their mate.

In summary, court-time for young females extended from March of their first year until they paired, on average, in February of their second year, a total of seven months (range: three to nine months). Minimum court-time for young males was thirteen months, but court-time for most young males was several years. Established pairs reunited quickly in the fall and had an average court-time of about 0.5 months (range: zero to two months). Court-time for re-pairing females appeared to vary depending on when they lost their previous mate and ranged from 0.5 to five months. Successfully re-pairing males had an average court-time of ten months (range: four months to more than several years). For both sexes then, court-time was longest for naïve, first-pairing birds, shortest for re-uniting birds, and intermediate for re-pairing birds. Males had longer court-times than females for first-pairing and re-pairing birds.

Pair-date was negatively related to court-rate for 2Y (Spearman correlation: r_s = - 0.55, $P_{1-tailed}$ = 0.008, N = 19) and 3Y (r_s = - 0.54, $P_{1-tailed}$ = 0.02, N = 14) females but not for A3Y females (r_s = 0.0, P = 1.0, N = 30) or A3Y males (r_s = 0.42, P = 0.2, N = 13). Pairing success of A3Y males was not related to their court-rate; considering only behavior prior to pairing, there was no significant difference in the court-rate of A3Y males who successfully paired (adjusted mean from a 2-way ANOVA including date-location: 61 ± 36 min d^{-1}) and those who failed to pair (74 ± 13 min d^{-1}) within that year ($F_{1,101}$ = 0.0, P = 1.0).

The amount of courtship received by particular females likely was in part due to male preferences. Before March, unpaired males appeared to ignore 1Y females. Three unpaired 2Y females observed at least five times during November-February were courted

during zero of six (binomial P = 0.001, given a probability of being courted of 0.32, see above), one of five, and six of six (P = 0.1) observation sessions, respectively, and differed in the mean time spent in courtship during that period (Kruskal-Wallis H_2 = 9.02, P = 0.01). One unpaired A3Y female was courted during each of seven sessions (Binomial test, P = 0.004, given a probability of being courted of 0.45).

Time-Activity Budgets

Significant seasonal differences were found in the proportions of time spent, and in the absolute amount of time spent per diurnal day, for all major behaviors (Table 3). Percent of the day devoted to feeding peaked in January and February, but the amount of time spent feeding per day peaked in March at sites where herring spawn was not available. Proportion and amount of time spent feeding in March where spawn was available was less than during all other months (Tukey post-hoc tests: P_s < 0.05). Birds spent more time resting, moving, and courting at spawning sites than elsewhere in March, and than during all other months (P_s < 0.05) except April for resting, October for moving, and October, November, and December for courting. Proportion and amount of time spent preening was less during December, January, and February than during all other months (P_s < 0.05) except October, and did not differ between spawning sites and elsewhere in March (P > 0.05). In all months birds spent only a few minutes of their day in aggressive interactions and vigilant behaviors. Frequency of agonistic interactions was highest during March at herring spawning sites than all other date-location categories (P_s < 0.05) and did not differ between other date-location categories (P_s > 0.05).

In addition to date-location effects, it was also important to determine whether age affected time budgets because unpaired birds tend to be younger birds and effects of pair status and age may be confounded. Differences by age were found for proportion of time spent in courtship by unpaired females

($F_{3,223}$ = 4.6, P = 0.004) and unpaired males ($F_{3,305}$ = 13.5, P < 0.001), time spent preening by unpaired males ($F_{3,305}$ = 5.8, P = 0.001), and time spent moving by unpaired males ($F_{3,305}$ = 6.9, P < 0.001). Proportion of time spent in courtship was less for 1Y females (0.4 ± 0.2%) and 1Y males (0.6 ± 0.3%) than older, unpaired females and males, respectively (Table 4; Tukey post-hocs, P_s < 0.05), time spent preening was greater for 1Y males (26.8 ± 3.8%) than older, unpaired males (Table 4; P_s < 0.05), and time spent moving was less for 1Y males (13.2 ± 2.2%) than older, unpaired males (Table 4; P_s < 0.05). There were no significant differences by age of unpaired females or males in proportions of time spent in other behaviors.

A 2-way ANOVA of the proportion of time spent feeding indicated significant effects due to date-location (Table 3), sex-pair (Table 4), and the date-location*sex-pair interaction ($F_{21,2563}$ = 2.1, P = 0.002). Differences by sex and paired status were due to lower feeding rates by unpaired males than other birds. Feeding rates by paired and unpaired females were similar (Table 4). Separate analyses were performed for the two sexes to help interpret the significant interaction effect. For females, no effect due to paired status was found ($F_{1,1234}$ = 0.2, P = 0.7), but the interaction of paired status*date-location was significant ($F_{5,1234}$ = 2.3, P = 0.04), and the proportion of time spent feeding in March at herring spawning sites was greater by unpaired (25 ± 4%, N = 49) than paired (13 ± 1%, N = 106) females (P = 0.03), while no differences were found between unpaired and paired females during other date categories (P_s > 0.05). A significant effect of paired status was found for males ($F_{1,1337}$ = 5.1, P = 0.02), but again the interaction of paired status*date-location was significant ($F_{5,1337}$ = 2.5, P = 0.03). Time spent feeding was less for unpaired (46 ± 2%, N = 349) than paired (55 ± 2%, N = 399) males during fall and winter (October to January), was greater for unpaired (20 ± 3%, N = 70) than paired (12 ± 1%, N = 98) males in March at herring spawning sites (P_s < 0.05), and did not differ between unpaired and paired males during other date categories (P_s > 0.05).

Table 3. Time-activity budgets of wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000. Proportions of time and absolute amount of time spent in each behavior, and the frequency of agonistic interactions, are presented. Listed values are means ± SEs, and statistical results for date-location differences are from a 2-way ANOVA model relating time spent to date-location and sex-paired status categories. In all months birds spent <1% of their day in aggressive and vigilant behaviors and only estimates of the amount of time spent are given for those activities.

Activity	Oct	Nov	Dec	Jan	Feb	March without spawn	March with spawn	Apr	ANOVA results F	ANOVA results P
No. of observations	144	401	247	649	341	216	323	288		
Proportion of time (%)										
Feeding	42 ± 3	50 ± 2	59 ± 2	61 ± 1	62 ± 2	56 ± 2	16 ± 1	42 ± 2	49.4	0.000
Resting	12 ± 2	7 ± 1	6 ± 1	3 ± 1	6 ± 1	10 ± 1	26 ± 2	24 ± 1	87.9	0.000
Preening	13 ± 2	19 ± 1	9 ± 1	9 ± 1	10 ± 1	18 ± 2	23 ± 1	15 ± 1	30.6	0.000
Moving	25 ± 2	19 ± 1	22 ± 2	22 ± 1	20 ± 1	14 ± 1	27 ± 1	17 ± 1	7.0	0.000
Courtship	8 ± 2	6 ± 1	5 ± 1	3 ± 0	2 ± 0	2 ± 0	7 ± 1	1 ± 0	8.4	0.000
Amount of time per diurnal day (min)										
Feeding	261 ± 19	280 ± 11	299 ± 12	327 ± 8	374 ± 10	399 ± 16	109 ± 7	346 ± 15	49.8	0.000
Resting	74 ± 12	38 ± 5	28 ± 6	17 ± 3	36 ± 5	71 ± 10	180 ± 10	199 ± 15	85.9	0.000
Preening	79 ± 11	109 ± 5	47 ± 7	49 ± 4	60 ± 6	132 ± 11	156 ± 8	120 ± 8	32.1	0.000
Moving	157 ± 13	105 ± 6	114 ± 8	119 ± 5	120 ± 7	99 ± 8	185 ± 9	142 ± 8	13.6	0.000
Courting	47 ± 9	33 ± 4	23 ± 4	18 ± 2	15 ± 2	11 ± 3	47 ± 6	6 ± 2	9.9	0.000
Aggressive interactions	1 ± 0	1 ± 0	1 ± 0	<1 ± 0	2 ± 0	3 ± 1	3 ± 1	2 ± 0	7.6	0.000
Vigilance	1 ± 0	2 ± 1	1 ± 1	0 ± 0	1 ± 0	1 ± 0	3 ± 1	2 ± 0	2.5	0.016
Frequency of agonistic interactions (no. h^{-1})										
All interactions	10 ± 2	7 ± 1	6 ± 2	7 ± 1	4 ± 1	3 ± 2	25 ± 1	10 ± 1	25.0	0.000

Table 4. Proportion of time and absolute amount of time spent during diurnal periods in various activities by wintering Harlequin Ducks in relation to sex and paired status. Listed are estimated marginal means ± SE from a 2-way ANOVA model relating time spent to date-location and sex-paired status categories. Different superscripts indicate significant differences between categories.

Activity	Unpaired female	Paired female	Unpaired male	Paired male	F	P
No. of observations	435	851	560	789		
Hours of observation	87.2	238.4	119.3	228.6		
Proportion of time (%)						
Feeding	51.0 ± 2.0^A	51.3 ± 1.3^A	43.9 ± 1.5^B	48.5 ± 1.4^A	4.6	0.003
Resting	8.8 ± 1.0^A	12.8 ± 0.7^B	10.0 ± 0.9^A	13.4 ± 0.8^B	6.8	0.000
Preening[a]	17.0 ± 1.1	14.6 ± 0.8	13.3 ± 1.0	13.1 ± 0.8	2.2	0.087
Moving[a]	17.1 ± 1.1^A	19.5 ± 0.8^A	25.8 ± 1.0^B	21.9 ± 0.8^C	16.0	0.000
Courtship[b]	9.6 ± 0.7^A	2.0 ± 0.4^B	9.5 ± 0.6^A	0.4 ± 0.5^C	118.1	0.000
Aggression to others	$<0.1 \pm 0.1^A$	$<0.1 \pm 0.0^A$	0.1 ± 0.0^A	0.6 ± 0.0^B	93.0	0.000
Victim of aggression	0.1 ± 0.0^A	$<0.1 \pm 0.0^B$	$<0.1 \pm 0.0^B$	$<0.1 \pm 0.0^C$	23.9	0.000
Vigilance	0.2 ± 0.1^{AB}	0.1 ± 0.1^A	0.4 ± 0.1^B	0.2 ± 0.1^A	3.9	0.009
Amount of time per diurnal day (min)						
Feeding	317 ± 12^A	316 ± 8^A	271 ± 9^B	298 ± 8^A	5.4	0.001
Resting	60 ± 7^A	87 ± 5^B	69 ± 6^A	92 ± 5^B	6.2	0.000
Preening[a]	107 ± 7^A	95 ± 5^{AB}	86 ± 6^B	84 ± 5^B	2.9	0.032
Moving[a]	106 ± 7^A	122 ± 5^A	161 ± 6^B	137 ± 5^C	14.1	0.000
Courtship[b]	59 ± 4^A	12 ± 3^B	59 ± 3^A	2 ± 3^C	88.8	0.000
Aggression to others	$<1 \pm 0^A$	$<1 \pm 0^A$	$<1 \pm 0^A$	4 ± 0^B	49.6	0.000
Victim of aggression	1 ± 0^A	$<1 \pm 0^B$	$<1 \pm 0^B$	$<1 \pm 0^C$	18.5	0.000
Vigilance	1 ± 0^{AB}	1 ± 0^A	2 ± 0^B	1 ± 0^A	2.8	0.041

[a]Excluding 1Y males (see text).
[b]Excluding 1Y males and known 1Y females (see text).

Paired birds of both sexes spent more time resting than unpaired birds (Table 4). When 1Y males were excluded (see above), amount of time, but not proportion of time spent preening differed significantly among sex-pair classes (Table 4). Females tended to preen more than males, but post-hoc tests indicated only that unpaired females spent more time preening than unpaired and paired males. No significant differences were apparent if 1Y males were included (see above). Time spent moving was greater for males than females, and greater for unpaired males than paired males (Table 4). Significant differences were the same and trends were only slightly less pronounced if 1Y males were included in the analysis of moving behavior.

Excluding 1Y males and known 1Y females, the analysis of the proportion of time spent in courtship showed significant effects due to date-location (Table 3), sex-pair (Table 4), and the date-location*sex-pair interaction ($F_{21,2488} = 4.0$, P < 0.001). Estimates of time spent in courtship by unpaired females were likely biased low relative to unpaired males because unmarked 1Y females could not be excluded from the analysis. Time spent in courtship was greater for unpaired than paired birds of both sexes, and was greater for paired females than paired males (Table 4). Separate analyses of paired and unpaired birds indicated that the significant interaction effect was due to greater time spent in courtship by paired females than paired males during October to January and during March at herring spawning sites ($P_s <$ 0.05), while there was little difference between paired females and males during February to April at sites without herring spawn ($P_s > 0.05$). Greatest differences were seen in October and in March at spawning sites when paired females and males were involved in courtship for 4.6 vs. 0.3% and 3.7 vs. 0.5% of their day, respectively. When paired females were being courted their mates attended them and were always part of the courting group, but the activity of males

at those times was considered part of mate defense rather than courtship (see below). Overall means (Table 3) underestimated the seasonal differences in courtship behavior for unpaired birds, especially during March at herring spawning sites. Time spent courting in March at spawning sites was higher ($18.0 \pm 2.4\%$ of diurnal time, or 126 ± 17 min d^{-1}) than during all other date-location categories when only unpaired, A1Y birds were considered ($F_{7,872} = 8.8$, $P < 0.001$; post-hoc: $P_s < 0.05$).

Paired males spent more time being aggressive and less time as the recipient of aggression than all other sex-pair classes, while unpaired females spent more time as the recipient of aggression than all other sex-pair classes (Table 4). Greater time spent by unpaired females as the recipient of aggression was likely due to their greater involvement in courtship (see below). In addition to the amount of time spent being aggressive (Table 4), paired males also spent 8 ± 1 min d^{-1} on average attending their mates but not behaving aggressively to other males while their mates were being courted. Total time spent by paired males in aggressive behavior and attending their mates was much less

than unpaired males spent in courtship (Table 4). Time spent in vigilant behavior was greater for unpaired males than paired females and paired males, and did not differ between paired and unpaired females nor between paired males and females (Table 4).

Many agonistic displays were associated with courtship and sex-pair differences in the frequency of interactions varied depending on whether courtship behavior was included or excluded (Table 5). Paired males directed signals at others more frequently and received signals less frequently than all other sex-pair classes if courtship behavior was excluded, while displays directed at others were more frequent by unpaired than paired males if signaling to females during courtship was included. Unpaired males were the recipients of displays more frequently than paired males, regardless of whether courtship behavior was included or excluded. Unpaired females received signals more frequently than paired females, but again these differences were due to interactions during courtship; outside of courtship there was little difference between unpaired and paired females in the number of interactions they initiated or received.

Table 5. Frequency of agonistic interactions among wintering Harlequin Ducks in relation to sex and paired status, including and excluding those performed during courtship. Listed are estimated marginal means ± SE from a 2-way ANOVA model relating number of interactions per hour to date-location and sex-paired status categories. Different superscripts indicate significant differences between categories. Sample sizes are given in Table 3. Chases between mates were included but low-intensity, intra-pair displays were excluded.

Type of interaction	Unpaired female	Paired female	Unpaired male	Paired male	ANOVA results	
					F	P
All agonistic displays including those performed during courtship (no. h^{-1})						
Directed at:						
Females	0.7 ± 0.3^{AC}	0.2 ± 0.2^{A}	7.6 ± 0.8^{B}	1.6 ± 0.7^{C}	38.2	0.000
Males	3.7 ± 0.6^{AC}	2.3 ± 0.4^{B}	3.6 ± 0.4^{AB}	5.1 ± 0.4^{C}	8.7	0.000
All recipients	5.1 ± 0.7^{A}	2.8 ± 0.5^{B}	11.2 ± 0.9^{C}	7.0 ± 0.8^{A}	23.5	0.000
Received from:						
Females	0.2 ± 0.0^{A}	$<0.1 \pm 0.0^{B}$	2.1 ± 0.4^{C}	0.1 ± 0.3^{AB}	15.3	0.000
Males	6.0 ± 0.8^{A}	1.6 ± 0.6^{B}	1.4 ± 0.2^{B}	0.2 ± 0.2^{C}	25.8	0.000
Other species	0.6 ± 0.1^{A}	0.3 ± 0.1^{B}	0.8 ± 0.1^{A}	0.3 ± 0.1^{B}	7.7	0.000
All sources	6.8 ± 0.8^{A}	1.9 ± 0.6^{B}	4.3 ± 0.5^{A}	0.6 ± 0.4^{C}	21.2	0.000
Total interactions	11.9 ± 1.1^{A}	4.7 ± 0.8^{B}	15.6 ± 1.2^{A}	7.6 ± 1.0^{C}	22.3	0.000
Agonistic displays excluding those performed during courtship (no. h^{-1})						
Directed at others	2.0 ± 0.5^{A}	2.6 ± 0.4^{A}	3.9 ± 0.4^{A}	5.4 ± 0.4^{B}	12.9	0.000
Received from others	1.6 ± 0.2^{A}	1.9 ± 0.2^{A}	2.6 ± 0.2^{A}	0.7 ± 0.2^{B}	16.4	0.000
Total interactions	3.6 ± 0.6^{A}	4.5 ± 0.4^{A}	6.5 ± 0.5^{B}	6.1 ± 0.4^{B}	5.2	0.001

DISCUSSION

Theory to account for variation in the timing of pairing, that primarily considered how phenotypic, social, and ecological factors affect male costs (Rohwer and Anderson 1988), poorly predicted pairing behavior in Harlequin Ducks (Table 1). The process of pair formation was protracted and there was no evidence that females preferred to pair as early as possible, except perhaps for re-uniting individuals, nor that pairing was delayed due to costs to males of courtship or mate defense. Newly-pairing females invested an extended period of time in courtship and mate sampling before pairing, in spite of an abundance of courting males clearly energetically capable of maintaining a pair bond. Many young females decided to pair during mid-winter when time constraints to males should have been most severe. When time constraints for males and females were relaxed during herring spawn, unpaired females did not immediately pair, but rather increased their courtship and mate-sampling rate (Rodway 2006) and paired gradually through and after the herring spawn period.

Many recent advances in our thinking about animal social systems have come from greater focus on female perspectives (Gowaty 1996, 1997; Jennions and Petrie 1997; Birkhead and Møller 1998), and in birds recent evidence suggests that resolution of reproductive conflicts between males and females favors female interests (Hughes 1998). Decisions by females about how much time and energy to allocate to the pairing process appeared to be the main factor controlling the timing of pairing in Harlequin Ducks. Time-budget trade-offs were apparent for young females and their date of pairing was related to the amount of time per day that they allocated to courtship. Pairing success of males was not related to their court-rate, nor was it likely related to the length of time they invested in courtship as they began courting while they were still immature and generally courted for several years before pairing.

Established pairs re-united in September, October, and early November, and females that had lost or divorced a mate re-paired at variable times throughout the winter, on average later than re-uniting birds and earlier than first-time pairing females, as predicted by the mutual-choice hypothesis. Females began courtship and mate sampling, forming liaisons with older males, at the age of nine months. Many females formed temporary liaisons and almost all formed more lasting pair bonds during their second winter, however some of those pair bonds also may have been temporary because some two-year-old females are seen unpaired on breeding streams (C. M. Smith, pers. comm.). Thus, some females engaged in courtship and trial liaisons with several males over a period of one to two years. Males began the pairing process earlier than females at only four or five months of age, but few paired before their fourth winter. Males also took longer to re-pair than females and some previously paired males remained unpaired for several years. Robertson *et al.* (1998) reported later pairing dates for all age groups than found in this study, but differences were likely due to larger sample sizes and more stringent requirements used in this study for estimating pair dates.

There was little evidence that paired females gained immediate benefits relative to unpaired females from mate defense and vigilance, as postulated by the male-costs hypothesis. Time spent feeding by unpaired and paired females did not differ except during March at herring spawning sites when unpaired females actually spent more time feeding than paired females. The only other differences in their time budgets were that paired females spent more time resting and unpaired females allocated more time to courtship, especially during herring spawn when less time was required for feeding. Lack of difference in time spent preening, and no increase in the allocation of time to preening by unpaired females during March at spawning sites, indicated that unpaired females were satisfying their requirements for body maintenance before allocating time to courtship. Unpaired females were capable of deterring courting males and there was no evidence that interference from males or requirements for vigilance reduced feeding

efficiency or increased predation risk for unpaired females. Time spent in vigilance behaviors differed neither between paired and unpaired females, nor between paired females and their mates. Thus, in terms of time budgets, costs to females of remaining unpaired appeared to be minor, and immediate benefits of becoming paired were not apparent beyond the obvious consequence that less investment in courtship was required.

Paired females were the recipient of aggressive displays less frequently than unpaired females, as predicted by the male-costs hypothesis, but those interactions occupied only about one min per day for unpaired females and the benefit for paired females was likely trivial, unless it was associated with a change in habitat use due to despotic behavior (Fretwell and Lucas 1970). This was unlikely because recipients of aggressive displays were not displaced from their immediate group (Rodway 2006), nor did unpaired females spend more time feeding than paired females as would be expected if they were forced into poorer quality habitats. Moreover, the greater frequency of interactions experienced by unpaired females was entirely due to their greater involvement in courtship and was not related to feeding or roosting habitats (Rodway 2006). Thus, for Harlequin Ducks there is no evidence that females increase foraging efficiency by becoming paired, either through greater time available for feeding or by gaining access to preferred food supplies through increased dominance status (Paulus 1983).

As measured by changes in time budgets, males stood to gain more from becoming paired than females. Unpaired males spent less time feeding and resting and more time moving, courting, as the recipient of aggressive interactions, and in vigilance and escape behaviors than paired males. Although paired males spent more time being aggressive to others than unpaired males, on average this only amounted to four min per day. Unpaired males spent much more time in courtship than paired males spent in mate defense. This was true in all winter months, even during mid-winter when time constraints were most severe. Constraints on

male time and energy budgets was not a plausible reason for delayed and protracted pairing of young and re-pairing females.

More time spent feeding by unpaired than paired birds during March at spawning sites could indicate higher energy costs for unpaired birds. More time allocated to courtship and moving could explain higher energy costs at that time (Ricklefs 1974). Alternatively, unpaired birds may have been in poorer body condition as a result of increased costs of courtship that were not offset by higher feeding rates through the winter. This latter explanation seems more likely true for unpaired males whose rate of feeding from October to January was reduced compared to paired males (this finding appears to contrast with that of Torres *et al.* (2002), but in fact Torres *et al.* reported almost identical, though not significant, differences in time spent feeding by unpaired and paired males when data were averaged over the entire winter). At that time, unpaired males appeared to allocate time to courtship and moving, likely in search of potential mates, partially at the expense of feeding time. This is further evidence that male constraints are not an important determinant of pairing chronology. Not only are unpaired males capable of bearing costs of courtship greater than those of mate defense by paired males, they also may be willing to incur an energy debt to increase their chances of obtaining a mate. Such time-budget decisions by unpaired males likely reflect sexual selection pressures through the mechanism of female choice that also have shaped the rapid molt sequence by males to return them to their nuptial plumage early in the fall (Cooke *et al.* 1997), the early start and persistent courtship by young males even though they will not pair for several years, and the fact that males bear almost all search and advertisement costs in the mate choice process (Rodway 2006).

This study has demonstrated that female Harlequin Ducks invest considerable time and energy into selecting a mate, and has indicated that the primary benefits of that investment do not accrue during winter. Similar results have been obtained in studies of

other migratory ducks (reviewed in Rodway 2007) and, although we cannot rule out possible benefits during the winter that have not been measured (species that maintain winter territories [Savard 1988] seem the most likely candidates for demonstrating winter benefits of early pairing, and warrant investigation), the apparent conclusion is that direct benefits of female mate choice in these species relate to improved mate co-ordination through time spent together on the wintering grounds, and to male behavior during migration or on the breeding ground. Indirect genetic benefits may also be important. Direct benefits may include hormonal synchrony and readiness for breeding (Bluhm *et al.* 1984; Bluhm 1988; Hirschenhauser *et al.* 1999), coordination of activities leading to successful migration, copulation, and fertilization, male defense and vigilance that increases foraging efficiency during the period of nutrient acquisition for egg-laying and incubation (Milne 1974; Ashcroft 1976; Sorenson 1992), establishment of a nesting site, and, in some species, defense of a nesting or foraging territory (Stewart and Titman 1980; Savard 1984; Gauthier 1987). Harlequin Ducks may have improved their co-ordination at copulation as paired birds copulated throughout the winter (October-April) on average once every two to three days (M. Rodway, unpubl. data), though this behavior also may have functioned in pair bond maintenance.

Mate choice criteria in Harlequin Ducks were not specifically investigated, but this study did reveal that male age and the possession of nasal discs (Regehr and Rodway 2003) affected female mate choice. Copulation or female solicitation to copulate by unpaired birds was never observed, suggesting that copulation did not serve in mate assessment. Pairing success of males was not related to the amount of time that they devoted to courtship, and female choice was likely based on more specific male traits and behaviors than just the total amount of time males had available for courtship. Unpaired females frequently rejected the advances of courting males and through agonistic displays were able to at least partially control whether and by whom they were courted

(Rodway 2004). However, amount of courtship directed at particular females, especially first-year females, also appeared to be partially a function of male mate-choice preferences, and female and male preferences likely interacted to regulate courtship behavior, number of potential mates sampled, and ultimately pair formation. Secondary reproductive strategies of FEPCs are pursued by paired males of many monogamous species, but females are not known to solicit EPCs, suggesting that benefits of protecting their chosen pair bond outweigh benefits of amending or complementing their mate choice decisions through EPCs (McKinney 1985; McKinney and Evarts 1997). Direct and indirect fitness benefits for females of most species are thus almost entirely dependent on their choice of mate prior to the breeding season.

The mutual-choice hypothesis was well supported by results of this study and provides a heuristic framework for future investigation. However, insights gained in this study of Harlequin Ducks would not have been possible without longitudinal data on marked birds. Long-term studies of other waterfowl species are needed to further test the hypotheses presented here and to elaborate the phenotypic, social, and ecological factors influencing pairing decisions in waterfowl. Detailed study of marked Harlequin Ducks has changed our perception of their mating system from seasonal monogamy (Johnsgard 1975) to long-term monogamy with low divorce rates (Rodway 2004). Similar revisions in our understanding of mating systems and pairing behavior of many waterfowl species may be expected as longer-term studies of known-age, marked birds with known pairing histories are conducted.

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