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

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 (   ), 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

1. ... *male costs* ... *mutual-choice* ... (...), ... (t-), ... (t- t), ... (200).

Male-costs predictions	Mutual-choice predictions	Available data (.)[a]	Harlequin Ducks (this study)
Pairing chronology: intra-specific trends			
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
No necessary trend	Court-time greater for naive than experienced birds	No data	Court-time greater for naïve birds
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			

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 *a*. 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
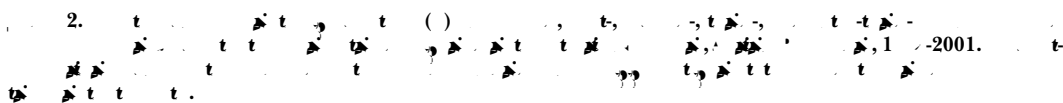
Month	Female age				Male age		
	1	2	3	>3	2	3	>3
Sept	0.0 (1)	0.0 (13)	0.0 (14)	2.0 (100)	0.0 (1)	0.0 (7)	1.8 (113)
Oct	0.0 (1)	9.1 (11)	20.0 (20)	51.9 (131)	0.0 (1)	9.1 (11)	39.3 (112)
Nov	0.0 (4)	5.3 (19)	55.6 (18)	77.4 (133)	0.0 (4)	9.1 (11)	54.2 (120)
Dec	0.0 (0)	0.0 (1)	61.5 (13)	98.0 (49)	0.0 (1)	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)

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 ±

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, $P_{1\text{-tailed}}$ = 0.008, N = 19) and 3Y (r_s = - 0.54, $P_{1\text{-tailed}}$ = 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).

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 =

Paired birds of both sexes spent more time resting than unpaired birds (Table 4).

at those times was considered part of mate

D

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

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 *a*. 1984; Bluhm 1988; Hirschenhauser *a*. 1999), co-ordination 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