Have Winter Spacing Patterns of Harlequin Ducks Been Partially Shaped by Sexual Selection?

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Abstract.—Sexual selection can operate throughout the annual cycle and likely shapes the winter plumage and courtship displays of many northern waterfowl that choose mates during winter. Less conspicuous effects of sexual selection are likely and in this study I asked whether winter distribution patterns and grouping behavior of Harlequin Ducks (*Histrionicus histrionicus*) are partially shaped by sexual selection. Harlequin Ducks are typically dispersed in small groups and observed grouping behavior supported the hypothesis that unpaired adult and immature birds will show sexually-selected changes in their spacing to facilitate courtship and mate sampling. Unpaired birds occurred in larger groups than paired birds during October-February, and group-related differences in the sex ratio and in the proportion of females that were unpaired indicated that unpaired birds were aggregating specifically for courtship. Behavior similar to lekking was observed at one site. Males gathered at this site at daybreak, unpaired females visited the site each apparently to attract a group of courting males, and these courting groups left the site without feeding. When herring spawn was available in March, unpaired birds were more likely to move to exploit it and gained both direct nutritional benefits as well as indirect benefits related to changes in time budgets and spacing behavior that facilitated courtship and mate sampling. Overall, results suggest that sexually-selected behaviors that affect the process of mate choice and the timing of pairing are important to consider if we are trying to explain winter spacing patterns of waterfowl. *Received 8 February 2006, accepted 9 August 2006.*

Key words.—courtship, delayed plumage maturation, grouping, Harlequin Duck, herring spawn, *Histrionicus histrionicus*, mate sampling, sex ratio, winter time budgets.

The effects of sexual selection on behavior have been intensely studied during mating seasons (Darwin 1871; Andersson 1994) but less so during non-reproductive periods (Møller 1994). Most northern waterfowl pair in winter (McKinney 1986) and we may expect behavioral adaptations facilitating mate sampling and mate choice at that time (Møller 1994; Höglund and Alatalo 1995). These adaptations may be considered sexually-selected to the extent that they represent advantages to individuals in competition with same-sex conspecifics in successfully pairing or in obtaining a higher-quality mate (Darwin 1871). Though sexually-selected behaviors are expected in males, and female distribution is considered largely determined by resource distribution (Emlen and Oring 1977), unpaired females also may develop behaviors that influence the quality of mate they obtain. In this study, I asked whether winter distribution patterns and grouping behavior of unpaired male and female Harlequin Ducks (*Histrionicus histrionicus*) are partially shaped by sexual selection.

Harlequin Ducks winter along rocky, marine shores, generally in small groups of 2-20 birds (Robertson and Goudie 1999). They have a monogamous mating system with no paternal care, male desertion during incubation, and form multi-year pair bonds on the wintering grounds (Gowans *et al.* 1997; Smith *et al.* 2000). Most females pair in their second year but males rarely pair before their fourth winter (Rodway 2004). They have a male-biased sex ratio of 1.5:1 in the Pacific Northwest (Rodway *et al.* 2003a) and, in males, have a variable Alternate I plumage that makes males identifiable throughout their first winter (Smith *et al.* 1998). Feeding takes a large proportion of their time during winter (Goudie and Ankney 1986; Torres *et al.* 2002). Their distribution on the Pacific coast changes in spring when a large segment of the population aggregates at sites where Pacific Herring (*Clupea pallasi*) spawn (Rodway *et al.* 2003b). Pair bonds are often formed at this time (Robertson *et al.* 1998; Rodway 2004). They are thus an appropriate species on which to test hypotheses about

sexually-selected changes in grouping behavior during the non-reproductive period.

Predictions were made about three aspects of Harlequin Duck winter behavior: (1) that unpaired birds will aggregate at mobile courting arenas (Johnsgard 1994) or at specific locations that would serve as "lekking" sites (Petrie 1989) to facilitate mate sampling; (2) that immature males will participate in courtship and show similar changes in grouping behavior as adult courting birds; and (3) that unpaired birds will be more likely than paired birds to move to locations where herring spawn because, in addition to nutritional benefits, unpaired birds will benefit from aggregations of conspecifics that will reduce costs of mate sampling, and from changes in time budgets that will allow them to allocate more time to courtship and mate sampling.

The study was conducted during October through April 1998-2001 at 22 wintering locations of Harlequin Ducks in the Strait of Georgia, British Columbia (details in Rodway *et al.* 2003a, b). Data were categorized into two location categories, areas where spawning by herring occurred and areas where herring spawning did not occur during the study, and seven date categories, October, November, December, January, February through to the beginning of herring spawning in early March each year (February), the 3-week period in March after herring spawning began each year (March), and from the end of the spawning period through April (April).

Grouping Behavior

Repeated surveys of Harlequin Ducks throughout study areas (details in Rodway *et al.* 2003a,b) were used to determine variation in group size and sex ratio. Birds were considered to be in separate groups if they were separated by ≥10 m. Changes were assessed in overall group size using unweighted means, and also using means weighted by the number of birds in each group to better reflect the proportion of total birds in each group size. Behavior of birds in different groups was determined by instantaneous scan sampling (Altmann 1974).

Comparisons were made of the proportions of females that were paired among different-sized groups in January, February, March, and April, and between locations. If a female and male remained in close proximity, behaved synchronously, and exhibited defensive reactions to intruders they were considered paired (Gowans *et al.* 1997). Individuals that showed no particular association with a potential partner were considered unpaired. Group size was determined when individuals were first sighted and thus females that were alone sometimes turned out to be paired. All females were

assessed to determine their pair status in small groups containing no more than 5 or 6 females, but in larger groups systematic sampling was used with a random start, varying the interval between females sampled according to the size of the group. For example, while scanning with a telescope across a large group of 2000 birds aggregated at herring spawn, every 5th female encountered in the scope field was selected, with a random start between 1 and 5, aiming for a sample size of about 100 females. Every 2nd female was sampled for smaller groups of about 30 birds. Each female selected was observed until their pair status was determined or until they had been observed for 5 min. Females whose pair status could not be confidently assigned after 5 min were excluded from the sample.

Sex and Age Ratios

Sex ratio was defined as the ratio of total males to total females. To analyze the relationship between sex ratio and group size, sex ratio was converted to the proportion of birds in a group that were male because sex ratio is constrained by group size. Male age ratio was the ratio of first-year (1Y) to after-first-year (A1Y) males. Birds were considered 1Y throughout their first winter. Birds were counted at locations where herring did and did not spawn during 2-week intervals from 4 weeks before to 8 weeks after herring spawning began to compare changes in sex and age ratios associated with herring spawn. Counts from different years, 1998-2001, were considered independent and were combined for analyses (*G*-tests). Conclusions were the same if years were considered separately. Alternate I plumage of a small sample of 1Y males was scored on a 5-point scale from juvenile-like to adult-like (details in Rodway *et al.* 2003a), to determine whether birds in more adult male-like plumage were more likely to engage in courtship than birds with more female-like plumage.

Behavioral Observations

About 3500 Harlequin Ducks have been captured and individually 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). Continuous observations of marked and unmarked focal birds (Altmann 1974) were conducted throughout daylight hours to determine time budgets, type and frequency of social interactions, and number of potential mates sampled. Most observation sessions were 5 min, but sessions in 1998 and some in 1999 were 30 min. Observations of marked birds were used to determine mate-sampling rates, and observations of both marked and unmarked birds were combined to determine daily time-activity budgets.

Duration to the nearest second of feeding, resting, preening, moving, and courtship behaviors, and frequency of agonistic interactions were recorded during each observation session. Absolute amount of time that birds spent in different behaviors per day 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. Numbers of daylight hours per day that birds were present was calculated as the time between sunrise and sunset adjusted by the median arrival or departure times relative to sunrise or sunset determined by Rodway and Cooke (2001) for each relevant

date category. Sunrise and sunset times for the study area were obtained from the U.S. Naval Observatory Astronomical Applications Data Services (U.S. Navy 2000).

Analyses

Proportional data were arcsine transformed to satisfy assumptions for parametric tests, except proportion of males in groups, which did not require transformation. There were no consistent differences in variances between 5 and 30 min observation sessions (Rodway 2004) and so they were combined for analyses. Variation in activity budgets was analyzed using full factorial ANOVA followed by Tukey *post hoc* tests for pairwise comparisons. Interaction terms were dropped from final models if they were not significant. Preliminary analyses indicated no consistent differences among location categories except during herring spawning. Thus, for subsequent analyses, data were combined from all locations for all date categories except during herring spawning, and a single date-location variable with 8 categories was used: 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) with four classes to test for differences among unpaired and paired females and males. 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. Tolerance for Type I error was set at 5% for all tests.

RESULTS

Grouping Behavior

Group size and mobile courting arenas.— Both unweighted and weighted mean group size differed dramatically between March at spawning sites and all other date-location categories (Table 1). March at spawning sites was excluded from the ANOVA model to test for differences among other date-location categories because variances for group size were extreme during that period. Excluding March at spawning sites, mean group size

was larger during April than during all other months October to March (unweighted means: $F_{6,5706}$ = 25.6, P < 0.001; weighted means: $F_{6,5706}$ = 180.2, P < 0.001; Tukey *post hoc*: all P < 0.001). Weighted mean group size also was larger during March at sites without spawning than during the months October to February (all P < 0.05).

Different sex-paired-status classes of birds were found in different-sized groups during January-February prior to herring spawning ($F_{4,2037}$ = 58.3, P < 0.001), but not during March at herring spawning sites ($F_{4,484}$ = 1.5, P = 0.2) or during April and March at sites without spawning ($F_{4,1236}$ = 2.0, P = 0.1). During January-February, mean group size that individuals were found in was larger for unpaired females (6.0 ± 3.6, N = 221), unpaired A1Y males (5.7 ± 3.8, N = 553), and unpaired 1Y males (5.2 ± 4.2, N = 100) than for paired females and males (3.6 ± 2.5, N = 584; Tukey *post hoc*: all P < 0.001). Although group size differed between unpaired and paired females only prior to herring spawning, the proportion of females that were unpaired differed among group-size categories in all months that it was measured: January ($F_{4,590}$ = 79.0, P < 0.001), February ($F_{5,1011}$ = 129.4, P < 0.001), March at sites without spawning ($F_{5,210}$ = 13.1, P < 0.001), March at spawning sites ($F_{7,108}$ = 8.2, P < 0.001), and April ($F_{4,74}$ = 10.0, P < 0.001). Except for single birds, highest proportions of females that were unpaired occurred in groups of 6-10 and 11-20 birds (Fig. 1). In all months, proportions that were unpaired were higher for single birds than all other group sizes, lower for groups of 2 than all other group sizes, and higher for groups of 6-10 than groups of 3-5, and, in February, higher for groups of 11-20 than groups of

Table 1. Changes in group sizes of wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000. Means ± SE are unweighted and weighted by the number of birds in each group.

Date	No. of groups	Unweighted mean	Weighted mean
Oct-Feb	4008	3.3 ± 0.1	5.9 ± 0.2
March without spawn	904	3.8 ± 0.2	13.3 ± 1.4
March with spawn	708	33.6 ± 7.2	1123.0 ± 258
April	801	7.5 ± 0.8	73.6 ± 12.5

3-5 (all P < 0.05). Mean group sizes did not differ between unpaired and paired females in March and April, likely because larger groups were more common at that time (Table 1, Fig. 1), while the proportion of females that were unpaired was highest in medium-sized groups.

The size of group an individual was in was related to its behavior during October-March, excluding sites in March with herring spawning (ANOVA model including date and location: $F_{3,6504}$ = 37.1, P < 0.001), but not during March at spawning sites ($F_{3,676}$ = 2.1, P = 0.1). During October-March, groups in which an individual was courting (7.7 ± 0.3, N = 492) or roosting (7.1 ± 0.3, N = 410) were larger than those in which it was feeding (4.7 ± 0.2, N = 1665) and than all sampled groups (4.7 ± 0.2, N = 1986; Tukey *post hoc*: all P < 0.001). Trends were the same for both unpaired and paired birds. Although similar in size, the composition of roosting groups differed from courting groups. Considering only group sizes >2 birds, the proportion of females that were unpaired was greater in groups of 6-10 than 3-5 for courtship ($F_{3,77}$ = 3.3, P = 0.03; *post hoc*: P < 0.05) but not for roosting ($F_{3,71}$ = 1.0, P = 0.4) behavior. Sex-ratio (analyzed as the proportion of males in a group) also differed among group sizes for courtship ($F_{3,228}$ = 4.7, P = 0.003; *post hoc*: P < 0.05) but not for roosting ($F_{4,203}$ = 0.3, P = 0.9) behavior, nor for all sampled groups ($F_{4,2921}$ = 0.6, P = 0.7). When an individual was courting, the proportion of males in the group was greater for groups of 6-10 birds (0.75 ± 0.02; sex ratio = 3.0 ± 0.1) than 3-5 birds (0.69 ± 0.02; sex ratio = 2.2 ± 0.1; P < 0.05). The operational sex ratio (analyzed as the proportion of unpaired birds that were males) increased from January to April ($F_{4,639}$ = 7.9, P < 0.001), and did not differ among group-size categories for all sampled groups ($F_{5,639}$ = 1.7, P = 0.1), nor for groups related to specific behaviors (e.g., courtship: $F_{3,62}$ = 0.2, P = 0.9).

There was no evidence that spacing was a result of agonistic interactions. Following an aggressive display, recipients generally moved not at all or only a small distance and remained within the same group, except for
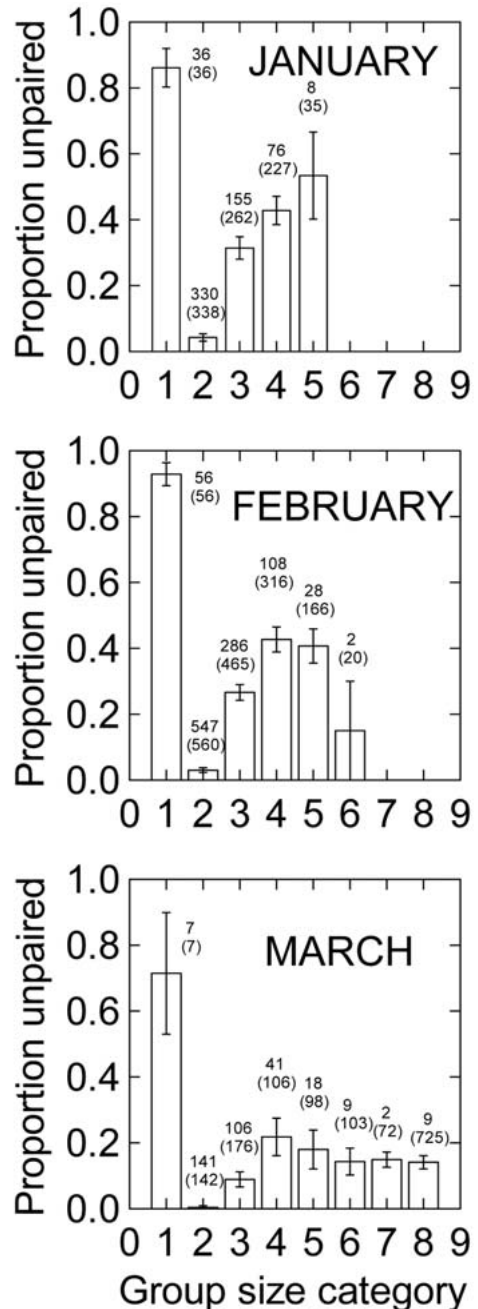

Figure 1. Mean proportion of Harlequin Duck females paired in different sized groups during January, February, and March 2000 in the Strait of Georgia, British Columbia. Note that March includes all sites where herring did and did not spawn, and April is not shown because proportion of females that were unpaired was very low in all groups but single birds at that time (maximum of 0.07 in groups of 3-5). Group size categories 1, 2, 3, 4, 5, 6, 7, and 8 represent groups of 1, 2, 3-5, 6-10, 11-20, 21-50, 51-100, and >100 birds, respectively. Standard errors are shown, and above bars are given the number of groups sampled and, in parentheses, the total number of females in those groups.

courting males that often left a group to pursue other females.

"Lekking sites".—Courtship occurred throughout the study area and throughout the day, but there was evidence of spatial and temporal differences in courtship rates. There were 20 sites for which there were at least 50 observation sessions per site. Birds spent more time courting at some sites than others ($F_{19,2379}$ = 4.5, P < 0.001) and during the morning prior to 1000 h PST than later in the day ($F_{4,2379}$ = 4.5, P = 0.001; Tukey *post hoc*: all P < 0.05), although the interaction of time*site was also significant ($F_{69,2379}$ = 2.0, P < 0.001) and some sites had higher rates of courtship at midday or later in the afternoon. Adjusted mean percent of time that birds spent courting at the different sites ranged from 0.6 ± 1.6 to 9.0 ± 0.9%. Four sites had significantly higher rates of courtship than other sites (all P < 0.05). One site in particular, Grassy Point on Hornby Island (49°33'N, 124°40'W), had significantly higher rates of courtship than more than 50% of the other sites. This site was used for feeding by groups of Harlequin Ducks throughout the day, including the morning time that aggregating, unpaired birds were courting, and had little to distinguish it from contiguous inter-tidal habitat except that it was a conspicuous point of land (though not the only one) in view of the offshore, nocturnal roosting grounds of most Harlequin Ducks in that area (Rodway and Cooke 2001).

High rates of courtship at Grassy Point were first noticed in fall 1999 and the site was visited 16 times after that to determine how birds used the site. Unpaired birds appeared to use Grassy Point as a rendezvous point in the morning, and unpaired females seemed to visit the site to attract a party of courting males, which they then led off in flight to other locations. Observations of 7 December were typical. The first birds to arrive were males, beginning at 0730 h, and by 0751 h there were 13 males, including two 1Y males, and 1 female roosting together on the point. By 0810 h, 25 males and 8 females had arrived, including three pairs which tended to remain separate from the large group of unpaired birds. The unpaired birds separated into courtship groups and by 0823 h the five unpaired females had flown off in separate courtship flights with four or five males each in tow, leaving only paired birds behind. Unpaired birds did not feed while they were at Grassy Point. This pattern of behavior was witnessed on 10 visits to Grassy Point at daybreak, during October-February. Sex ratio at Grassy Point in these early-morning flocks (3.1 ± 0.3, N = 8) was higher than expected (based on a population sex-ratio of 1.51; combined probability, χ^2_{16} = 33.6, P = 0.006), and higher than later in the day (1.5 ± 0.1, N = 8); number of birds present was higher in the morning before 0800 h (36 ± 9) than at other times of day after 1000 h (12 ± 3; t_{14} = 3.5, P = 0.004).

This type of phenomenon was not observed at 15 other sites visited at daybreak. Concurrent observations, with the help of an assistant, at Grassy Point and a nearby site called "Squeaker" on 29 October highlighted the differences in behavior at these sites. By 0830 h, 32 males and 9 females, one of which was paired, had congregated at Grassy Point, and seven males and five females (four paired) had gathered at Squeaker. Except for the one paired female, all the females at Grassy Point left in separate courtship flights, each with 3-7 males in tow. First feeding at Grassy point began at 0919 h after the initial courting groups had left and six new birds were present, while all the birds at Squeaker were feeding by 0835 h and, with the addition of one male, were still present at 1000 h.

Behavior of 1Y males.—1Y males were observed courting throughout winter, although the overall proportion of time spent in courtship was less for 1Y males (0.6 ± 0.3%; N = 68) than older, unpaired males (10.2 ± 0.8%; N = 246; $F_{3,305}$ = 13.5, P < 0.001). First-year males did not appear to be excluded from courtship or other groups, and in fact may have been more tolerated than older males. Based on the proportion of 1Y males in the population (Rodway *et al.* 2003a) and the total number of displays directed at males (Table 2), 1Y males were the target of aggressive displays less frequently than would be expected from paired (G_1 = 96.0, P < 0.001)

Table 2. Relative frequencies of aggressive displays performed by wintering Harlequin Ducks in relation to their sex, age [hatch-year (1Y) and after-hatch-year (A1Y)], and paired status, and to the target of the display. All displays between mates were excluded.

Displays	Unpaired female	Unpaired 1Y male	Unpaired A1Y male	Paired female	Paired male
Number of displays	325.0	108.0	715.0	594.0	1477.0
Directed at females (%)	16.6	26.9	52.7	9.6	6.2
Directed at 1Y males (%)	5.5	9.3	1.3	7.6	1.2
Directed at A1Y males (%)	77.8	63.9	46.0	82.8	92.7

and unpaired ($G_1 = 12.6$, $P < 0.001$) males, and not different from that expected from paired ($G_1 = 0.1$, $P = 0.7$) and unpaired ($G_1 = 0.9$, $P = 0.3$) females. 1Y males with different plumage scores that were observed in courtship (2 each with plumage scores 2, 3 and 4) suggested that plumage did not affect whether a 1Y male participated in courtship.

Herring Spawn

Time budgets.—Time spent feeding was lower ($F_{7,872} = 14.1$, $P < 0.001$; Tukey *post hoc*: all $P < 0.05$) and time spent courting was higher ($F_{7,872} = 8.8$, $P < 0.001$; Tukey *post hoc*: all $P < 0.05$) in March at spawning sites than during all other date-location categories for unpaired, A1Y birds (Fig. 2). Those birds also allocated more time to resting and moving, but not to preening, during March at spawning sites in comparison with birds at sites where herring did not spawn (Fig. 3).

Sex ratio.—Male bias in the sex ratio increased during March at spawning sites when herring spawn became available (Fig. 4). Sex ratio was higher during the first 2-week interval of the spawn period than during the previous 2-week interval at locations where herring spawned ($G_1 = 6.05$, $P = 0.007$) but not at locations where herring did not spawn ($G_1 = 0.21$, $P = 0.65$). Male bias in the sex ratio was greater at locations where herring spawned than where herring did not spawn during the first ($G_1 = 3.42$, $P = 0.032$) and second ($G_1 = 7.94$, $P = 0.003$) 2-week intervals after herring first spawned. Increased male-biased sex ratios associated with herring spawn were not due to increases in the proportion of immature males because male age ratios did not increase until after the

spawn period (Fig. 4) when paired birds began to depart to breeding grounds.

Pair status.—Proportions of females that were unpaired were similar at locations where herring did and did not spawn in the periods 3-4 weeks (19.5%, N = 493 vs. 20.9%, N = 230; $G_1 = 0.2$, $P = 0.7$) and 1-2 weeks (10.9%, N = 46 vs. 11.3%, N = 115; $G_1 = 0.01$, $P = 0.9$) before spawning began, but were greater at locations where herring did than did not spawn in the period 1-2 weeks after spawning began (11.6%, N = 432 vs. 5.6%, N = 142; $G_1 = 4.65$, $P = 0.016$). Proportions were similar at locations with and without spawn in the period 3-4 weeks after spawning began (10.2%, N = 127 vs. 8.0%, N = 176; $G_1 = 0.5$, $P = 0.5$).

Mate sampling.—Number of males courting a female at any one time differed among
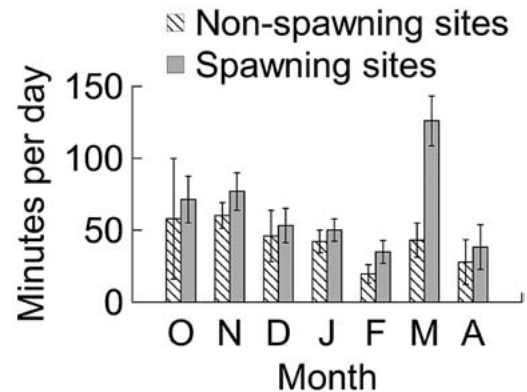

Figure 2. Comparison of seasonal trends from October to April in the amount of diurnal time spent in courtship by unpaired, greater-than-one-year-old Harlequin Ducks between locations where herring spawned in March and locations where herring did not spawn, in the Strait of Georgia, British Columbia, 1998-2001. Bars depict means ± SE.
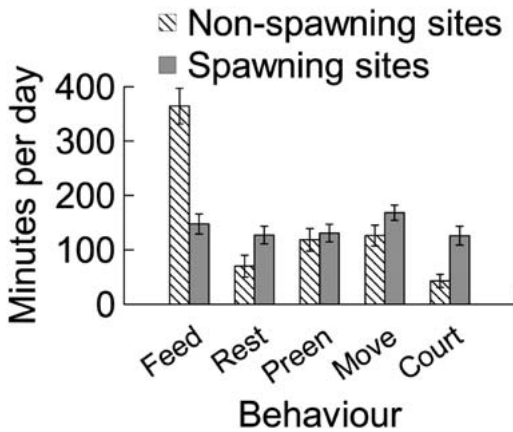
Figure 3. Allocation of time to different behaviors by unpaired, greater-than-one-year-old Harlequin Ducks during March at locations where herring did and did not spawn, in the Strait of Georgia, British Columbia, 1998-2001. Bars depict means ± SE.
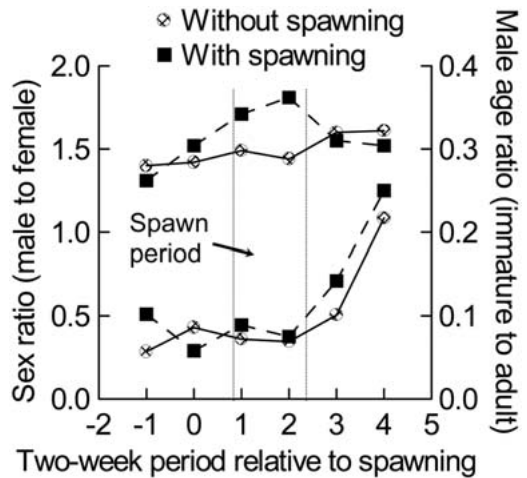

Figure 4. Comparison of trends in Harlequin Duck sex ratios (upper lines) and male age ratios (lower lines) between locations where herring spawned and locations where herring did not spawn in the Strait of Georgia, British Columbia, 1998-2001. The period when spawn was available to Harlequin Ducks at spawning sites is enclosed in vertical, dotted lines. Sample sizes were 732 and 530, 1241 and 477, 4958 and 428, 1499 and 480, 1988 and 395, and 312 and 434 adult males at locations where herring did and did not spawn, during consecutive, two-week intervals, respectively.

date-location categories ($F_{7,662} = 6.1$, P < 0.001), and was higher during March at spawning sites (5.0 ± 0.3, N = 31) than during January (3.6 ± 0.1, N = 200), February (3.3 ± 0.2, N = 136), and April (3.1 ± 0.4, N = 22; Tukey *post hoc*: all P < 0.05), but not than during March at sites without spawning (4.3 ± 0.3, N = 44), nor during October (3.7 ± 0.3, N = 29), November (4.1 ± 0.2, N = 116), or December (4.3 ± 0.2, N = 92; all P > 0.05). Because only a small proportion of males were marked, the total number of males courting a female per day could not be determined. A maximum of 18 males courting a single female was observed during March at spawning sites, but as many as 10 males pursuing a female was seen in all months of the study.

Number of females courted by an unpaired male during an observation session also differed among date-location categories ($F_{7,203} = 3.7$, P = 0.001), and was higher during March at spawning sites (2.2 ± 0.2, N = 30) than during all other date-location categories (Tukey *post hoc*: all P < 0.05; overall mean = 1.4 ± 0.1, N = 182). Focal males courted as many as five different females during a single, 5-min observation session. During March at spawning sites, 81% (N = 42) and 100% (N = 17) of females courted by unpaired and paired males, respectively, were paired, although per encounter during a

5-min observation session, unpaired males spent longer courting unpaired females (4.2 ± 0.4 min) than paired females (0.7 ± 0.2 min; $t_{12} = 2.8$, P = 0.02).

DISCUSSION

Grouping behavior of Harlequin Ducks supported the hypothesis that unpaired birds will show sexually-selected changes in their spacing to reduce the costs of mate sampling. Individuals looking for mates in dispersed populations will incur greater movement costs than more gregarious species and may find it difficult to compare the quality of potential partners (Jennions and Petrie 1997). This will be especially true in species like Harlequin Ducks with long-term pair bonds and late in the pairing season because as established pairs are removed from the mating pool the number and density of potential partners declines. As in lek-mating systems, females may prefer larger aggregations where potential mates can be sampled concurrently (Emlen and Oring 1977; Brad-

bury 1981; Lank and Smith 1992), leading to the observed aggregations of unpaired birds at mobile courting arenas (Johnsgard 1994) and at specific locations that served as "lekking" sites (Petrie 1989).

Unpaired birds occurred in larger groups than paired birds during October-February. Results suggested that there was an optimal group size for courting birds, in the order of 6-20 birds, and a greater proportion of females were unpaired in those sizes of groups in all months that it was measured, even during March and April when mean group sizes were much larger. Birds gathered in larger groups for courtship and roosting than for other behaviors. However, the reasons for larger group sizes likely differed for courtship and roosting behavior because the proportion of females that were unpaired and the male bias in the sex ratio were greater in larger groups when a focal bird was courting but not when it was roosting, indicating that unpaired birds were aggregating specifically for courtship. Operational sex ratio did not vary among group sizes, even for courtship, suggesting that unpaired males were distributed in an ideal-free fashion (Fretwell and Lucas 1970) with respect to unpaired females. This is what we would predict unless unpaired females are assorted according to their attractiveness to males.

Spacing patterns could not be explained by exclusion of unpaired birds by more dominant pairs, as has been observed in other non-territorial, mobile groups of wintering waterfowl (e.g., Black and Owen 1989), because recipients of aggressive displays were not displaced from their immediate group. Further, there is no reason to expect that unpaired birds would occur in larger groups even if they were being displaced by despotic behavior of paired birds. Possible greater benefits to unpaired birds of predator defense (Wittenberger and Hunt 1985) or information transfer (Ward and Zahavi 1973), perhaps because they are in poorer shape than paired birds, could lead to aggregation of unpaired birds. However, such benefits would be unlikely to result in segregation based on paired status only for courtship and not when birds are roosting or feeding. The only hypothesis consistent with the observed aggregation of unpaired birds specifically for courtship is that these spacing patterns have been sexually selected to facilitate mate sampling.

Lekking-like behavior was observed early in the morning at one location. Males gathered at this site at daybreak, unpaired females visited the site each apparently to attract a group of courting males, and females came for no other obvious purpose because these courting groups left the site without feeding. The behavior was observed at this site during two winters, indicating that there was something unique about the site and that the behavior was not just a temporary habit of a few birds. Such behavior may be more widespread and additional sites will need to be discovered before we can determine what location features serve to attract courting birds and whether such aggregations can be explained by hotspot or female choice models used to explain traditional lekking behavior (Höglund and Alatalo 1995). As far as I know, such behavior has not previously been reported for any waterfowl species, but we may expect unpaired birds to exhibit similar behavior in other dispersed populations and perhaps in more densely flocking species when the majority of birds are already paired.

Grouping behavior of immature males was similar to that of other unpaired birds, and immature males participated in courtship throughout their first winter, though at a lower rate than adult males. Displays of young male waterfowl are less developed than adults (Dane and Van der Kloot 1964; Korschgen and Fredrickson 1976; Afton and Sayler 1982) and immature males may accompany adult courting birds to gain exposure to and experience in courtship so as to improve their display skills. Involvement of immature males in courtship, even those with female-like plumage, and lower-than-expected rates of aggression directed at first-year males from adult paired and unpaired males, provide some support for the hypothesis that delayed plumage maturation acts as an honest signal of subordination that minimizes aggressive interactions with adult males and allows young males to gain experi-

ence in courtship (Lyon and Montgomerie 1986). Male-biased sex ratios in many duck species may result in directional selection on males to begin courtship as early as possible if participating in courtship increases the probability that a young male will pair successfully later in life.

Individuals of many species often time their life history events to coincide with predictable but ephemeral food abundance (e.g., Botton *et al.* 1994), but little attention has been paid to possible indirect benefits of exploiting such resources. Aggregating at herring spawning sites in March provided birds with both direct nutritional benefits (Rodway *et al.* 2003b; Rodway and Cooke 2002) and indirect benefits related to changes in time budgets and spacing behavior. Time required for feeding was dramatically reduced for all birds feeding on spawn and unpaired birds allocated much of their spare time to courtship and moving, likely in search of potential mates. Data indicated that unpaired birds were more likely to come to herring spawning sites than paired birds; proportion of females that were unpaired was higher at herring spawning sites than elsewhere during the first but not the second two-week interval that spawn was available, and male bias in the sex ratio was higher at spawning sites throughout the time spawn was available. These patterns would be expected if unpaired birds were preferentially moving to spawning sites at the start of the spawning period and then forming pair bonds while they were there. Rodway *et al.* (2003b) found that the proportion of Harlequin Ducks moving to herring spawning sites was strongly related to the distance that birds had to travel, suggesting that there were trade-offs between the costs of moving and the benefits of exploiting herring spawn. If so, then greater proportions of unpaired than paired birds moving to spawn suggests that unpaired birds were willing to incur higher movement costs to gain indirect benefits associated with pairing activities. One telling observation is that the farthest known travel distance of 150 km by a Harlequin Duck moving to a spawning site (Rodway *et al.* 2003b) was performed by a divorcing, >6-year-old female, that had been

paired for at least two years prior to moving, and that left her previous mate behind in a small wintering population of <100 birds where there would have been few alternate mate choices (Rodway 2004).

Higher proportions of unpaired females and greater male-biased sex ratio at spawning sites than elsewhere during the first two weeks of spawn would also result if all birds were equally likely to come to spawning sites but unpaired birds stayed longer than paired birds. Several lines of evidence rule against this possibility and support the conclusion that unpaired birds were more likely to move to herring spawning sites than paired birds. First, tracking of marked birds and counts of wintering populations showed that most paired birds returned to their wintering areas after visiting spawning sites and were not departing early for breeding grounds (Rodway *et al.* 2003b). Second, male age ratio did not increase during the spawning period. Finally, proportions of unpaired females during the second two-week spawn period and male age ratios throughout the spawning period were similar at spawning and nonspawning sites.

Alternative explanations for why unpaired birds were more likely to visit spawn areas than paired birds may be that paired birds are generally more attached to their traditional wintering grounds and are less liable to move (Robertson *et al.* 1999, 2000; Cooke *et al.* 2000), or that unpaired birds are in poorer condition and gain greater benefit from feeding on spawn than paired birds. The former explanation seems least plausible because most of the wintering population moves to herring spawning sites (Rodway *et al.* 2003b) and the vast majority of birds moving are paired (Rodway 2004). The latter explanation gains some support from the fact that, although all birds spent very little time foraging at spawning sites, unpaired birds did spend more time feeding than paired birds (Rodway 2004). However, there is no evidence that unpaired birds were in poorer condition than paired birds through the winter (Rodway 2004; Torres *et al.* 2002), and higher feeding rates by unpaired birds at spawning sites can most parsimoniously be

explained by their need to offset the requirements of allocating more time to the energetically expensive activities of courtship and mate sampling at that time. Given that the operational sex ratio did not vary among sites during herring spawn, it seems reasonable to conclude that the difference in proportions of unpaired females and males between areas with and without spawn was driven by the sexually-selected, preferential movement of unpaired females followed by unpaired males to spawning sites.

Contrary to expectations, unpaired birds were not more aggregated during herring spawn than paired birds, and courtship groups were similar in size during March at spawning sites as elsewhere at that time and as during October through December. However, the proximity of large numbers of birds at spawning sites (Rodway *et al.* 2003b) would have decreased sampling costs for birds searching for mates, and may have functioned analogously to the "lekking" site that unpaired birds used through the winter as a rendezvous point from which they departed in social courtship groups. Decreased costs were most apparent for unpaired males that had higher rates of mate sampling during March at spawning sites than during any other date-location category. Although numbers of males courting a female at any particular time was not exceptional during herring spawning, females likely also had higher rates of mate sampling at herring spawning sites due to a greater turnover of males in courting groups.

Most of the females courted by males at herring spawn were paired, but unpaired males spent only brief intervals courting paired females and focused most of their courtship on unpaired females. This suggests that males required a brief assessment period to determine that a female was paired. Support for this possibility comes from frequent observations throughout the winter of flying, unpaired males alighting and briefly courting a paired female that was diving a small distance away from her mate. Such unpaired males generally ceased courting the female and often flew off again when the paired male intervened, although it was

not uncommon for an unpaired male to stay and feed with a pair for a while. On several occasions, flying, unpaired males performed similar behavior with single female Surf Scoters (*Melanitta perspicillata*), flying away again after a brief assessment, as if realizing their mistake. This behavior was more costly away from spawning sites because of the greater travel distance between females.

More time for mate sampling and coincidental access to large numbers of potential partners that could be readily compared at herring spawning sites likely increased the quality and compatibility of mates obtained by pairing birds (Real 1990; Sullivan 1994; Mazalov *et al.* 1996; Jennions and Petrie 1997; Johnstone 1997), although it is possible that herring spawn is a poor time for mate assessment because differences in male quality will be less apparent when time and energy budgets are relatively unconstrained. Although most females were paired before March, 50% of second-year females forming their first pair bonds and a small proportion of older, re-pairing females formed pair bonds during or after the herring spawning period (Rodway 2004). Because pair bonds are long-term, herring spawn may thus provide important indirect benefits that increase the fitness of over 50% of the breeding population through its effects on individual mate choice opportunities and decisions.

In waterfowl, female choice is likely the primary mechanism of sexual selection because male dominance rank is most commonly unrelated to pairing success (reviewed in Rodway 2004). The process of mate choice is an important determinant of pairing chronology in waterfowl and winter pairing may be partially an adaptation to reduce time constraints on female mate choice that has been selected because of the benefits of accurately assessing variation in male behavioral characteristics (Rodway 2004). Effects of sexual selection are obvious in Harlequin Ducks; adult males regain their nuptial plumage early in the fall after a brief eclipse plumage (Cooke *et al.* 1997), and males bear costs of search, advertisement, and competition for mates throughout the winter and for several years (Rodway 2004).

Females also bear costs of mate sampling and assessment over a protracted courtship and trial liaison period lasting months or even years (Rodway 2004). Less obvious effects were demonstrated in this study showing that grouping and movement of unpaired and immature birds are behaviors at least partially shaped by sexual selection.

Adaptive changes in grouping behavior related to pairing had not previously been investigated in waterfowl. However, additional support for the idea comes from studies of Wood Ducks (*Aix sponsa*), that are typically dispersed in small groups, showing that group size and male bias in the sex ratio during autumn were greater for courting than other groups (Armbruster 1982). Northern Pintails (*Anas acuta*) also exhibited greater courtship in larger groups, but at a much larger scale, with most courtship occurring in groups >5,000 birds (Miller 1985; Migoya *et al.* 1994). Data suggest that sexually-selected behaviors that affect the process of mate choice and the timing of pairing are important to consider if we are trying to explain winter spacing patterns of waterfowl. Individual decisions about habitat use and pairing are likely inter-related and should be considered together in future investigations of distribution and sexual- or age-related segregation of wintering waterfowl.

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Associate Editor: Jean-Pierre Savard.