

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

MICHAEL S. RODWAY¹

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

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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.

STUDY AREA AND METHODS

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

3-5 (all $P < 0.05$). Mean group sizes did not

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

—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 q -test: 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 $9.0 \pm 0.9\%$. Four sites had significantly higher rates of courtship than other sites (all $P < 0.05$). One site in particular, Grassy Point on Hornby Island ($49^{\circ}33'N$, $124^{\circ}40'W$), 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, $\chi^2_{16} = 33.6$, $P = 0.006$), 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.

—1Y males were observed courting throughout winter, although the overall proportion of time spent in courtship was less for 1Y males ($0.6 \pm 0.3\%$; $N = 68$) than older, unpaired males ($10.2 \pm 0.8\%$; $N = 246$; $F_{3,305} = 13.5$, $P < 0.001$). 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 ($G_1 = 96.0$, $P < 0.001$)

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 spent feeding was lower ($F_{7,872} = 14.1$, $P < 0.001$; Tukey q : all $P < 0.05$) and time spent courting was higher ($F_{7,872} = 8.8$, $P < 0.001$; Tukey q : 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

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 q -test: 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

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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 hy-

pothesis 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

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 non-spawning 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 (Cooke *et al.* 1997), 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 (), 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 () 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 pair-

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