

BEHAVIOUR AND CHRONOLOGY OF PAIR FORMATION BY HARLEQUIN DUCKS *HISTRIONICUS HISTRIONICUS*

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The chronology of pairing and behaviours associated with pairing were studied on a small population of wintering Harlequin Ducks. Research was carried out on 17 days between 19 September and 21 November 1995 on a 2 km rocky coastline in south-western British Columbia. The behaviours rushing, agonistic pursuits and head-nodding were found to be specific to courtship. Males performed more courtship behaviour than females. Males which had completed their pre-alternate moult exhibited courtship behaviours more often than moulting males. Pairing began in mid-September and continued to increase steadily to between 44% and 70% of females paired by 21 November. Three pairs identified during the 1994-1995 non-breeding season, re-united in the fall of 1995. Harlequin Ducks pair relatively early, probably because many pairs are re-uniting in the fall. The courtship behaviour shown by males is probably mate guarding by paired males and active courtship by bachelor males.

Keywords: Harlequin Duck, Timing of Pairing, Pairing Behaviour, Moult, Pair Re-union

Unlike most bird species, many duck species, particularly those nesting in temperate and arctic regions, form pair-bonds up to seven months in advance of breeding (Oring & Saylor 1992). Among the well-studied migratory ducks of the northern hemisphere, males are thought to be unable to economically defend breeding territories, due to the ephemeral nature of waterfowl breeding areas (Rohwer & Anderson 1988). This leads to a mate-defense mating system (Emlen & Oring 1977) which may uncouple pair formation from the breeding grounds. Duck populations are often male-biased (Sargeant *et al.* 1992) making sexual selection for available females a strong factor in waterfowl behaviour. Females may benefit from early pairing by having mates defend them during intra-specific interactions. These factors may lead to directional selection for continuously earlier pairing until a balance is reached with other selective forces.

Among duck species there is considerable variation in the timing of pairing over the

winter months, from early fall as in Mallards *Anas platyrhynchos* to late spring pairing in Lesser Scaups *Aythya affinis* (Weller 1965). A variety of explanations has been proposed as possible correlates of earlier pairing which include; larger body size (Rohwer & Anderson 1988), poor forage quality (Paulus 1983), sex ratios (Hepp & Hair 1984) and the timing of breeding (Weller 1965).

The most basic aspects of pairing behaviour in the sea ducks (tribe: Mergini) have yet to be intensively researched. Courtship behaviours have been described for some of the species, most notably the elaborate displays of the three members of the genus *Bucephala* (Cramp & Simmons 1977, Afton & Saylor 1982). The precise chronology of pairing has been studied in only a few species (Ashcroft 1976, Afton & Saylor 1982, Savard 1985).

Little is known about pairing behaviour and the timing of pairing in Harlequin Ducks *Histrionicus histrionicus*. Harlequin Ducks breed in mountain streams and winter along rocky

coastlines. They are seasonally monogamous with some evidence of pair-bond renewal from breeding ground data (Bengtson 1972). Relatively few observations of pair-forming behaviour in Harlequin Ducks have been made, and the descriptions have often not been in close agreement (Johnsgard 1975, 1978). Many social behaviours may be associated with courtship display such as *head-nodding* in both sexes and *bill-dipping*, *lateral bill-shaking*, *rushing* and *preening* in males (Johnsgard 1975, Fleischner 1983, Inglis *et al.* 1989). Johnsgard (1975) stated that the only female sexual display recognised to date was *inciting* which rarely had been seen. Pair-bond maintenance behaviours are described by Inglis *et al.* (1989) and Fleischner (1983). Many different sequences of copulation have been observed (Inglis *et al.* 1989). Copulations, however, are not usually observed at the wintering site (Fleischner 1983).

This study sought to identify the specific behaviours and social factors that are associated with or initiate pair-bonding in Harlequin Ducks on their wintering grounds. The specific objectives of this study were to: 1) identify and describe behaviours associated with pair formation in Harlequin Ducks; 2) determine whether male and female Harlequin Ducks have different behavioural repertoires; 3) determine whether courtship activities occur during the pre-alternate body moult or when full plumage has been acquired; 4) describe the seasonal chronology of pair formation in Harlequin Ducks; and 5) document any cases of pair re-union.

Study area

The study was carried out west of White Rock, in south-western British Columbia, on an exposed rocky stretch of shoreline approximately 2 km long. A population of up to 100 Harlequin Ducks moult and winter at this site. Access to this site is provided by a 4 m high railway dyke, which stretches along the entire shoreline. The intertidal zone is composed of coarse gravel in the low areas bordered by boulders in the high areas along the dyke. The rock boulders provide above

water platforms during mid-tide for Harlequin Ducks to haul out as they are prone to do during the daylight hours. Harlequin Ducks exhibit within-site fidelity and are not observed locally outside of this area due to unsuitable habitat (Robertson *et al.* in press). Harlequin Ducks are present at this site all year long. Immature birds may remain at the wintering grounds for the entire year. Adult males and females depart for the breeding grounds (sub-alpine streams and rivers) in late spring. The males and some unsuccessful females return to their coastal wintering areas in the middle of the summer, leaving the females to incubate and raise their broods. The females and the juveniles return to the coast in the late summer and early fall (Palmer 1976).

Methods

After a brief pre-study assessment of their behaviour related to tide changes, data were collected during mid-tide when Harlequin Ducks would be close to shore or hauled out. Field data were collected, using binoculars and a spotting scope, from the dyke at the shoreline. Observations were made after a slow approach, which rarely disturbed the birds. Date, weather conditions, time of day and tide status were recorded at the beginning of each field day.

Location, sex, and proximity to other conspecifics were recorded for all individuals. Males were aged by plumage characteristics as hatch year or adult birds if possible (Palmer 1976). The age of females was not distinguishable from field observations of plumage. One-minute focal sampling intervals were carried out on each bird sighted in which all unique behaviours performed by the individual were recorded (see below for behavioural descriptions). If legs were visible, banding status was determined and, if possible, the tarsal band code recorded (see Robertson *et al.*, in press, for details of banding programme). Moult status, either pre-alternate moult or full alternate plumage, was assessed for each male.

Male-female pairs were identified where possible and records were kept as to where

and when they were observed. Values for minimum total pairs were based on a conservative set of data where it was confident that all data within this set represented a true pair. Confidence for these values was given by observation of constant proximity, synchronous activity and behaviour orientation directed by both birds towards each other (McKinney 1992). Maximum values of total pairs were taken from a data set that represented all possible pairs with and without the confidence to identify them as such. Some assumptions were made in this latter data set which included, for example, two males and one female observed in a group were assumed to represent a pair with one unpaired male; or as another example, a group consisting of three males and three females were assumed to consist of three pairs.

Behaviour descriptions

The following is a list of observed behaviours whose descriptions are adapted from McKinney (1965), Johnsgard (1975), Palmer (1976), Fleischner (1983), and Inglis *et al.* (1989).

Courtship Behaviours

Agonistic Pursuits: Aggression toward members of either sex by a female, or toward members of the same sex by males, in the form of skidding forward through the water, the body, head and neck extended forward and usually accompanied by vocalizations.

Rushing: directed movement toward females by males, in the same form as "agonistic pursuits" (above) but of slightly longer duration, skidding forward through the water, the body, head and neck extended forward, usually accompanied by vocalizations.

Head-nod: Extension of the head up and forward in an elliptical movement as a form of social communication assumed to be associated with courtship.

Maintenance Behaviours

Preening: Distribution of oil from the uropygial gland over the plumage with the head and chin,

combing and rubbing the feathers of the body with the bill or nibbling the base of the feathers and the skin.

Resting: Bill under the wing along the back, or the body stationary in a standing or squat position with head low and no other obvious movements, occurring either on the surface of the water or while hauled out.

Tail-wag: Repeated vigorous lateral movement of the tail from left to right. Generally performed as a maintenance behaviour but may also have been a social or courtship behaviour, although not differentiated.

Wing-flap: Extension and forward beating of both wings while the breast and belly are lifted out of the water. May also have been performed as a social or courtship behaviour but not differentiated as such.

Splash-bathing: Splashing the body in the water while vigorously beating the wings and undulating the head and body just under the surface, often with the complete up-ending of the body into the water for one or two seconds.

Feeding Behaviour

Food-handling: Processing prey in the bill when diving or dabbling.

Diving: Partial opening of the wings followed by a rapid leap forward into the water, swimming fully below the surface of the water for up to 30 seconds.

Peering: Dipping most of the head momentarily below the surface of the water as though searching for food or predators.

Dabbling: Feeding along the shoreline in shallow water, dipping the head and neck into the water to grasp benthic organisms while swimming. Observed only at low tide.

Other Behaviours

Swimming: Active movement across the surface of the water.

Flying: Taking or ending flight while in view.

Alert: An erect posture of the head while standing or squatting, with attention to sound or sight in the immediate environment.

Additional behaviours such as wing and leg stretches, scratching, head-shaking, inciting, and water-flicking (Johnsgard, 1965) were observed but not during sampling intervals. Whether or not birds were hauled out of the water was also noted.

Data analysis

General data manipulation and analysis were completed with SAS statistical software (SAS Institute Inc. 1990). Spearman's correlation coefficients were calculated within individual birds to examine whether courtship behaviours were associated with each other, and with the other behaviours. The behaviour data was subdivided into six consecutive 10-day periods and surveys within a period were pooled. Behaviours were pooled into courtship, feeding and maintenance categories; alert, hauling-out, swimming and flying were analyzed separately. *P* values of less than 0.05 were considered significant, although *P* values of less than 0.10 were described as marginally significant as a compromise between type I and type II errors.

Results

On average 59 birds (24 to 76) birds were surveyed. The average population size was 27 (11 to 42) females and 33 (13 to 45) males. In the beginning of the study, females (a few of which may have been juvenile males) often

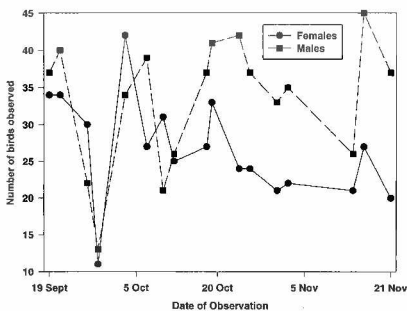


Figure 1. Number of males and females present at each survey.

dominated the population, but by mid-October all surveys were male biased (**Figure 1**).

Behaviour

Within individual males, all of three of the courtship behaviours, rushing, agonistic pursuit and head-nodding, were positively correlated with each other ($r_s=0.104$ to 0.273 ; $P=0.02$ to 0.0001 ; $n=490$). Within individual females agonistic pursuit was positively correlated with head-nodding ($r_s=0.245$; $P=0.0001$; $n=447$) (females did not engage in rushing, by our definition). Within individual males, swimming ($r_s=0.201$; $P=0.0001$; $n=490$) and flying ($r_s=0.113$, $P=0.012$) were positively correlated with courtship activities. Within individual females other behaviours were not correlated with courtship activities ($r_s < 0.056$; $P>0.23$; $n=447$). The proportion of birds involved in courtship activities was not correlated with the proportion of birds engaged in any other behaviours ($P>0.1$, $n=17$).

Figure 2 shows the proportion of birds engaging in each of the seven different behaviours grouped over time for each sex. The proportion of males exhibiting courtship behaviour increased over the study period but there was no change for females (**Table 1**). More males were seen feeding as the season progressed. Different proportions of females were seen feeding over the study with no apparent trend (**Table 1**). The number of males engaged in maintenance behaviours varied over the study, although no variation was detected in females. The number of males alert appeared to decrease over the study. The frequency of this behaviour did not change over time in females. Males showed a decreased likelihood to haul out later in the season. In females, this behaviour varied, however, there was no obvious trend over the season. No temporal variation in the proportion of birds swimming was seen. The number of birds seen flying varied significantly over the study (**Table 1**).

A higher proportion of males than females were engaged in courtship activities (**Table 2**). Males also tended to swim and fly more frequently than females (**Table 2**). The proportion of birds engaged in the other behaviours did not differ between the sexes.

Table 1. Chi-square statistics examining temporal heterogeneity (G) and linear trends (Mantel-Maenszel χ^2) in the percentage of individuals exhibiting specific behaviours. Raw values are presented in Figure 1.

Behaviour	Females				Males			
	G	P	M-H χ^2	P	G	P	M-H χ^2	P
Courtship	7.29	0.200	0.016	0.900	15.92	0.007	6.118	0.013
Feeding	19.81	0.001	2.66	0.103	31.24	0.001	15.99	0.001
Maintenance	8.31	0.140	0.004	0.950	13.09	0.022	2.151	0.143
Alert	8.18	0.147	2.62	0.105	22.75	0.001	9.56	0.002
Hauling-out	12.48	0.029	1.13	0.288	34.39	0.001	14.89	0.001
Swimming	2.71	0.744	0.361	0.548	8.92	0.112	0.127	0.721
Flying	11.94	0.036	0.926	0.336	13.14	0.022	1.038	0.308

Table 2. Chi-square statistics examining sexual differences in the proportion of birds exhibiting specific behaviours. See Figure 1.

Behaviour	G	P
Courtship	66.09	0.001
Feeding	0.891	0.345
Maintenance	1.286	0.257
Alert	0.121	0.728
Hauling-out	0.265	0.607
Swimming	10.45	0.001
Flying	5.69	0.017

Moult status

Males which had completed their moult engaged in general feeding behaviours more than males still undergoing their pre-alternate moult (Table 3). Moulting males tended to haul-out of the water more often. Moulting males were not observed flying. Although only marginally significant, males which had completed their moult engaged in courtship activities more often than males in pre-alternate moult (Table 3).

Pairing chronology

The first confident observation of pairing was on 26 September. The percentage of paired females is presented in Figure 3. The highest

minimum estimate of the proportion of paired females during the study period was 44% (possibly to a maximum 70%) and occurred on 16 November. The high percentage values on 28 September, (27% of females were seen paired), is attributed to a low bird population on that day (only 24 individuals).

Pair re-union

Three pairs were identified in the fall of 1995 that had also been documented as pairs in the 1994-1995 season. In another five pairs, in which the male of the pair was banded in 1994-1995 and the female was unbanded, the males were seen with either an unbanded or newly (fall 1995) banded female. No cases of divorce and re-pairing with new mates were detected. At least three pairs (38%) from the previous year re-united (Rowley 1983), and potentially eight pairs (100% of birds with sufficient data to detect pair-bond breakage) re-united.

A single copulation was observed on 16 November between an unbanded male and unbanded female pair.

Discussion

Courtship behaviour

The aggressiveness and competitive skills of males are essential to successful pair formation (McKinney 1992). Johnsgard (1965, 1978)

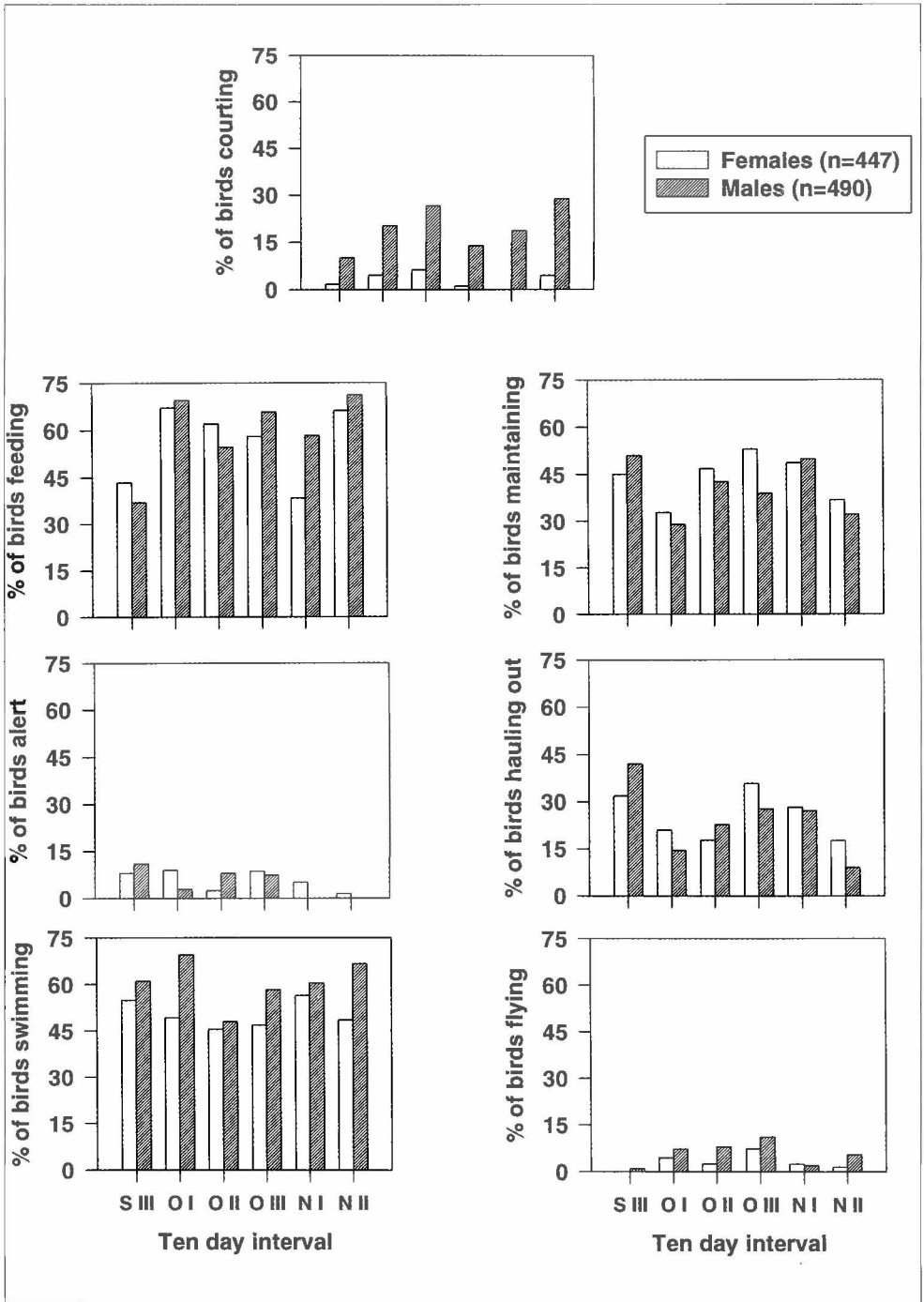


Figure 2. Percentage of birds exhibiting each behaviour during the one-minute focal sample.

Table 3. Percentage of male Harlequin Ducks exhibiting each behaviour grouped into birds still moulting or having completed the pre-alternate moult. Data collected past 12 October were excluded as all males had completed the pre-alternate body moult.

Behaviour	Pre-alternate moult (n=49)	Complete (n=104)	G	P
Courtship	6.1	15.8	2.93	0.087
Feeding	42.9	64.4	6.31	0.012
Maintenance	51.0	37.5	2.49	0.115
Alert	6.1	6.7	0.02	0.886
Hauling-out	42.9	26.0	4.31	0.038
Swimming	57.1	56.7	0.002	0.962
Flying	0.0	7.69	6.38	0.012

describes head-nodding as the primary male sexual and aggressive display used in situations of courtship and often accompanied by a high-pitched single or trilled vocalization. He also states that aggressive rushes toward other individuals have frequently been observed as well as repeated wing-flapping and lateral bill-shaking. In this study, a correlation existed within individual males between rushing, head-nodding and agonistic pursuit. Swimming and flying were also correlated with courtship activities. The act of rushing females was a common behaviour performed by males during

courtship and was assumed to be the primary courtship behaviour.

A typical courtship sequence began with one or more bachelor males either swimming or flying into an area and rushing an unpaired female. Groups of three or four males would often 'mob-rush' a female, following her for relatively long periods of time during which the female would dive and swim in random directions, apparently to avoid them. These mobs would often change individuals during the course of the vigorous activity, some leaving to feed as other new individuals joined the group. Females would respond by vocalizing and rushing away, seemingly disturbed. The female never appeared receptive. She would dive, evading the male(s), who would attempt to dive after her, jostling for position amongst themselves. Occasionally she would behave aggressively towards them before diving. If she was initially hauled out on a rock, the confrontation would usually be short-term and she would again settle on a nearby rock. If in the water, the confrontation would generally continue longer. It is uncertain whether the female was actually paired with one of the males in these groups and that this behaviour was a type of mate-guarding or pair-bond maintenance (McKinney 1992) in which the paired male was establishing dominance over the female and the other bachelor males. Male interactions were agonistic during these group encounters. Some of these incidents might be perceived as indirect pairing behaviour in response to competition for females. Females

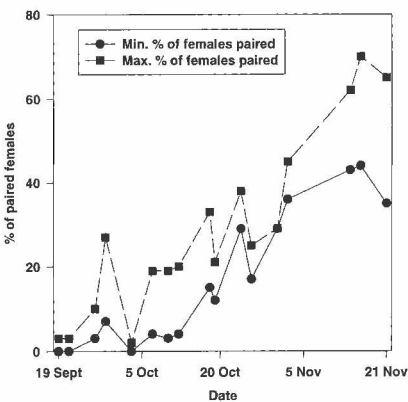


Figure 3. Minimum and maximum percentage of paired females seen at each survey.

responded to threats and disturbances by behaving aggressively towards other birds of both sexes, although it is possible that one might also interpret some of these agonistic events as courtship behaviour.

Vocalizations were very common but unfortunately not monitored for evidence of their specific relationships to courtship behaviours. They are considered a more important means of communication in Harlequins than in most species of ducks (Fleischner 1983). Different sounds were made by males than females, the female expressing a low, coarse pitch and the male a high, squeaky pitch. Male vocalizations varied in length, intensity and trill between behaviours. A larger vocal repertoire probably compensates for a small repertoire of visual displays (Fleischner 1983, Inglis *et al.* 1989) and may be important in pairing events.

During the non-breeding season, a general pattern of reproductive behaviour occurs, from initiation of the pairing process until most females are paired. Courtship activity, in the beginning, is infrequent and then becomes progressively more frequent until the number of displays begins to decline again (Hepp & Hair 1983). This pattern of increasing reproductive behaviour exhibited in wintering male Harlequin Ducks, however, was not apparent in the females. In addition, females were consistently more passive than males in their pairing performances and in their responses to the efforts of males to attract their attention, showing no tendency to adjust their relative activity. Males vigorously displayed singly or in 'courting parties' (McKinney 1992) while females simply swam, dove or struggled to maintain their position on a rock while being disturbed by other individuals. Although there were some instances of female head-nodding, only one observation of inciting was recorded. During this event, the female swam repeatedly into a group of resting males eliciting periodic mild aggression among the males. She did not vocalize but waited each time at the boundary of the group for them to settle down again, apparently seeking some particular response. Eventually she was driven away by two of the males who then returned to their resting position.

Moult, courtship behaviour and feeding

Since pair-bonds in Harlequin Ducks are seasonal, it is reasonable to assume that the mating system is related to moult pattern. Full alternate plumage serves as a signal of prime condition and reproductive readiness facilitating mate choice by females (Hohman *et al.* 1992). In this study, males in pre-alternate moult engaged in fewer courtship activities than full plumage males, which supports the theory that moult condition is a criterion for mate-choice. They also spent more time hauled out, less time feeding, and were not observed flying. It is possible that searching for females and subsequent rushing and sexual displays are taxing for males and so justifies the higher incidences of feeding in males who had completed their moult. Alternatively, moulting males may not have fed as often because, while diving, new feathers offer poor insulation and there is a risk of feather damage.

The proportion of males feeding increased during the study. There are a variety of reasons why males might feed more. Harlequin Ducks are obligate diurnal foragers (Goudie & Ankney 1986). As the day length decreases with approaching winter, available foraging time is reduced. Coupled with deteriorating weather conditions, Harlequin Ducks must increase their time spent foraging during the shorter day to maintain their body condition. The need for replenishment after moult is a possible factor in the increased foraging of male Harlequin Ducks, however, most studies have shown that the energetic cost of moult is easily met by normal foraging behaviour (Ankney 1984, Hohman *et al.* 1992). Courtship behaviour may be energetically costly and males may need to increase foraging to acquire enough energy to perform these behaviours. Females, however, do not show an increase in foraging behaviour. Either they are foraging at a higher rate to begin with, or they do not need as much food, as they are not engaging in costly courtship behaviours. Other studies have shown that males in good condition acquire mates sooner and engage in courtship behaviours more often (Paulus 1983, Wishart 1983, Brodsky & Weatherhead 1985, Hepp 1988).

The timing of pair formation may be dependent on the completion of pre-alternate moult and the attainment of full alternate plumage by males. In other species of ducks, males attaining their full plumage earliest form the first pair-bonds (Wishart 1983, McKinney 1992, but see Hohman & Ankney 1994). Hepp & Hair (1983), in their study of five species of dabbling ducks, found that the timing of reproductive behaviour was closely related to the attainment of full alternate plumage and that species which developed alternate plumage late began courtship later and paired later.

Pairing chronology and pair re-union

Harlequin Ducks pair early in the non-breeding season. At least half of the females were paired by November. Early pairing by waterfowl has received considerable attention in literature (Rohwer & Anderson 1988, Anderson *et al.* 1992). Females are a limiting resource for males, as waterfowl populations are generally male-biased. Exhibiting higher parental investment than males, females are scarcer due to mortality related to parental care (Oring & Saylor 1992). A primary argument for the function of the pair-bond during winter is that it provides increased foraging time for females (Ashcroft 1976). Vigilant males watch for predators and guard against disturbance by conspecifics, thereby allowing their mates to spend more time foraging (Oring & Saylor 1992). Thus females can impose selective pressure on males to pair earlier than they might if mates were not limiting. If males could detect quality or condition differences among potential mates, there would be selection for even earlier mate acquisition (Anderson *et al.* 1992) as males compete for limited females. In males, early pairing provides opportunities to enhance mate survival and fecundity and might be considered an indirect investment of parental care via the mate (Oring & Saylor 1992). Competition for food may also influence early pairing.

Another important factor affecting the timing of pair-bond formation is the advantages that paired waterfowl may have over unpaired individuals of a population. Paired ducks are

dominant to unpaired conspecifics and paired females participate in aggression less frequently than unpaired females because they are protected by their mates (Ashcroft 1976, Wishart 1983, Paulus 1983, Hepp 1984). Superior dominance rank of paired individuals, resulting from early pair formation, is beneficial to wintering ducks due to preferential access to resources (Hepp 1984, 1988). Earlier paired birds may accumulate greater energy reserves for reproduction. The best time of pair-bond formation usually is the product of a complex set of selective forces that change with time (Hepp 1988) and a combination of all these factors is probably responsible for early winter pairing in Harlequin Ducks.

Johnsgard (1968) stated that in ducks which mate every year, there is probably little re-mating with same individuals, owing to the break-up of pairs in late spring, the high annual mortality rate, and a general shuffling of flocks during migration. This is clearly not the case in Harlequin Ducks. Observations at the breeding grounds, have shown that Harlequin Ducks reform the same pairs in subsequent seasons (Bengtson 1972). This is the first study to show that, in Harlequin Ducks, pairs re-unite on the wintering grounds. Savard (1985) documented the occurrence of pair re-union in wintering Barrow's Goldeneye *Bucephala islandica*, another species within the tribe Mergini. In his study he stated the possible advantages of pair re-union over the formation of new pair-bonds were 1) obtaining an experienced mate of known abilities; 2) familiarity of the males with the territory; and 3) reduction of the time and energy spent in courtship. Wintering site fidelity in Harlequin Ducks (Breault & Savard, in press) may facilitate the re-union of individuals with their previous mate.

Compared to many duck species Harlequin Ducks pair relatively early. Pochards *Anas Penelope*, for example, are thought to pair later (not until late winter, early spring) because they obtain their food by diving (Rohwer & Anderson 1988). Diving is an energetically expensive foraging technique, which may preclude individuals from courting during months when they are expending all of their reserves to maintain body condition.

Additionally, males cannot follow a female while diving, hence mate-guarding is not feasible. Harlequin Ducks also dive for food but pair in the fall, hence, diving for food does not appear to constrain them from early pairing as is observed in the Pochards. Pair re-union is probably an over-riding factor in the establishment of early pair-bonds in Harlequin Ducks. Harlequin Ducks that re-unite obtain an experienced mate and do not waste energy in potentially costly courtship behaviour. In fact, much of the courtship behaviour seen in the fall may actually be mate-guarding activities. Although male Harlequin Ducks do not appear to defend territories, they do defend their mates from conspecifics (Inglis *et al.* 1989). In Eiders *Somateria mollissima* paired females forage more than unpaired females (Ashcroft 1976). Advantages conferred by pair re-union, coupled with the advantages of having a male to defend the female, all select for early pair-formation in Harlequin Ducks.

Copulation sequence

Copulation, in some duck tribes, may occasionally be performed in the fall (Johnsgard 1968). In Mallards, copulation may occur between relative strangers before pair formation and often appears to have little relationship to pairing (Johnsgard 1968) although, McKinney (1992) states that 'winter copulations' could aid in potential mate assessment and strengthen pair-bonds. In Harlequin Ducks, copulation has been described in several different ways. Most observations have been at the breeding grounds and have involved aggressive manoeuvres by males to initiate copulation with the female. Pre-copulatory behaviours have included repeated rushing by the male towards the female while 'squeaking' (Johnsgard 1965). This may be repeated several times before mounting is achieved. Others have observed behaviours such as mutual head-nodding and bill-dipping, upward-stretches of the body (Johnsgard 1965, 1975, Inglis *et al.* 1989) and head-throwing by the male before copulation (Johnsgard 1975). Fleischner (1983) stated that copulation among Harlequin Ducks

at the wintering grounds had been reported only once before. In the present study, the male's behaviour was relatively passive. While swimming towards the shoreline, the male repeatedly circled the female, constantly vocalizing or 'mouse-squeaking'. For five minutes the female swam idly watching him circle her. Eventually she assumed the prone position on the water and the male immediately treaded her, successfully copulating. The female croaked once during copulation and upon completion both birds flapped their wings and then dove. After surfacing, they swam along the shoreline for five minutes, the male still vocalizing, and then both hauled-out where she croaked once again while he continued to vocalize. They were hauled out for approximately five minutes and then flew east, the male still continuing to vocalize.

Conclusion

Results presented information which confirmed the typical behaviours of wintering Harlequin Ducks and contributed to the identification of specific pairing behaviours, including winter copulation. Differing significant trends were found in all behaviours, including pairing behaviours, between the sexes and over the season. Male Harlequin Ducks were the courting sex, expending considerable effort to pair with relatively passive females. The completion of the pre-alternate moult was a factor in the initiation of courtship behaviour. Pairing began early in the winter, and pair re-union occurs on the wintering grounds. In long-lived seaducks the following excerpt is highly relevant. "There is a need for studies of long-term relationships among individuals who know each other and have histories of interaction. Long-term relationships may influence the costs and benefits of interactions in ways that make no sense to one observing interacting individuals for the first time" (Anderson and Titman, 1992). The knowledge that pairs re-unite with a high frequency suggests that much of the courtship behaviour seen in Harlequin Ducks may be mate guarding and active courtship by bachelor males.

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