The pre-nesting behaviour and time budget of the Harlequin Duck *Histrionicus histrionicus*

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We describe the behaviour patterns, time budgets, diurnal rhythms and spacing patterns of the Harlequin Duck in the pre-nesting period. The study area was on the Laxá, a river in northeast Iceland, where the population is at a high density, containing pairs and unpaired males in the ratio 2:1. Birds spent much of their time resting on islands close to the water and dived for food in the fast stretches of the river. Females sat and preened more than males. They also had longer dive times. Agonistic and pre- and post-copulation displays are described. Males were not territorial but guarded their mates vigorously. Females incited their mates and joined them in agonistic encounters. Extra-pair copulation by paired males was not observed and unpaired males spent little time attempting to copulate with females. These mating strategies are discussed in the context of anatid strategies generally. The displays and time budget data are related to those of other ducks that inhabit fast-flowing rivers.

Throughout its breeding range in eastern Siberia, North America, Greenland and Iceland the Harlequin Duck *Histrionicus histrionicus* lives only on turbulent streams and rivers, often at high altitudes. Amongst the ducks it shares this breeding niche with only a few southern hemisphere species: the Torrent Duck *Merganetta armata* (Scott 1954, Johnson 1963, Wright 1965, Johnsgard 1966, Moffet 1970, Eldridge 1979, 1986a), the Blue Duck *Hymenolaimus malacorhynchos* (Kear & Burton 1971, Kear & Steel 1971, Kear 1972, Eldridge 1985, 1986b) and Salvadori's Duck *Anas waigiuensis* (Kear 1975). The Harlequin is thought not to be closely related to these other species (e.g. Cramp & Simmons 1977) and a comparison of behaviour might, therefore, indicate the importance of their specialised niche in shaping displays and time budgets. Unfortunately very little is known of Salvadori's Duck, and relatively little has been published on the behaviour of the Harlequin (the major papers being those of Bengtson 1966, 1972). The aim of this study was to help fill this gap for the Harlequin by providing quantitative data on the breeding time budgets and displays during the pre-nesting period. Data for nesting time budgets and behaviour will be published separately (Lazarus & Torrance in prep.). We also discuss the implications of our findings for male and female reproductive strategies, including mate guarding and extra-pair copulation.

The study was conducted on the major Icelandic breeding area of the Harlequin, near Lake Mývatn in northeast Iceland. The birds do not spend all year on the mountain rivers but overwinter (from September to April) on the sea around steep cliffs and rocky headlands (Gudmundsson 1961). The ducks migrate up the breeding rivers in late April and begin to lay in mid May, with a peak of laying in early June. The females incubate alone and males leave the rivers for the return trip to the sea in late June. The females and ducklings migrate down the rivers in early September.

Methods

Observations were made from two hides erected on steep hillsides overlooking adjacent stretches of the Laxá River approximately 6 km downstream of its exit from Lake Mývatn. At this point the river runs swiftly over a lava field and contains a multitude of protruding rocks and many islands (Fig. 1), some vegetated with dwarf willow. Maps were drawn of the two areas

Figure 1. A group of male Harlequins resting on rocks in a fast-flowing section of the Laxa. After females have started laying, the males gather in all-male groups before moving down the river to the sea.

with the major islands and groups of rocks numbered. Every hour a scan was made by checking the various sections of the river in a standard sequence using X20 – X60 telescopes. Between scans, data on social interactions were gathered opportunistically. Observations were made in the pre-nesting period from the second week of May until the first week in June. Data were gathered in 1978 with additional data on agonistic and sexual interactions being obtained in 1980.

On each scan the location, sex, breeding status and behaviour were noted for every individual, as well as the distance and status of the first and second nearest neighbours. Behaviour was recorded as general locomotory activities (i.e. sit, stand, walk, swim and fly) and more specific behaviours that could occur with one or more activity (see below). The height of the hides above the river meant that it was difficult to hear any but the loudest vocalization above the noise of the rapids. Each scan record consisted of information either from a solitary male (we had only three records of an apparently unpaired female) or from both members of a pair. Data were gathered for all 24 hours of the day, with a mean of 68.6 (SE ± 0.9) records per hour.

Although we could not identify individuals, we must have sampled the same birds many times (though rarely in the same hour) particularly during those parts of the day when the ducks are most sedentary. There is no satisfactory way of eliminating this replicated-subject bias when conducting significance tests; however, the conservative probability level of 0.01, two-tailed, has been adopted for all tests. Means are shown ± their standard errors.

Results

Bird numbers

Figure 2 shows the hourly variation in the mean number of Harlequin pairs per day, and of unpaired Harlequin males per day. There were usually about twice as many pairs as solitary males within our monitored stretches of the river, and this ratio is in line with surveys conducted on the Laxá by

Bengtson (1966). The numbers dropped around midnight when many ducks flew up the Laxá to roost on sand spits near the river's exit from Lake Mývatn.

The Harlequin was by far the most common duck species observed within our study areas (1646 scan records out of a total of 1711). Mallard *Anas platyrhynchos* accounted for 31 records (13 pairs and 18 solitary males). They confined their activity to feeding in the few calm, muddy bays in the river bank and never ventured into the current. By contrast Barrow's Goldeneyes *Bucephala islandica* were seen on 12 scans swimming in fast water (eight pairs and four solitary males). However these birds were far more common in slightly slower stretches of the Laxá near the river's exit from the lake. Other species observed were Wigeon *Anas penelope* (four pairs and three solitary males), Gadwall *Anas strepera* (four pairs and two solitary males) Scaup *Aythya marila* (five pairs), Teal *Anas crecca* (two pairs and a single male) and Pintail *A. acuta* (one pair).

Habitat preferences

The ducks spent much of the day (47%) on the banks of the larger islands, rarely venturing more than 1 m from the water until nest prospecting began. Densely vegetated banks were avoided and sandy beaches in the lee of the islands were preferred. Less time (24%) was spent on the rocks that protruded from the river and very little time (<1%) on the banks of the Laxá itself, where the ducks were more at risk from ground predators (e.g. Arctic foxes, mink). For the remainder of the time (28%) the Harlequins swam on the river. Of the 628 records of swimming birds, 43% were in 'calm' water, 51% in 'fast' water and 6% in 'white' water. Within the two study areas 4% of the river was calm, 86% fast and 10% white water. Although the ducks therefore spent a larger proportion of their swimming time than expected ($X_2^2 = 42.4$, $P<0.001$) in calm water, they preferred to feed in the faster stretches of the river (see below).

General activity

Table 1 summarizes the activity data for unpaired males, paired males and paired females (as already stated we had only three records of a seemingly unpaired female). The ducks were very sedentary, spending a large part of the day sitting or standing.

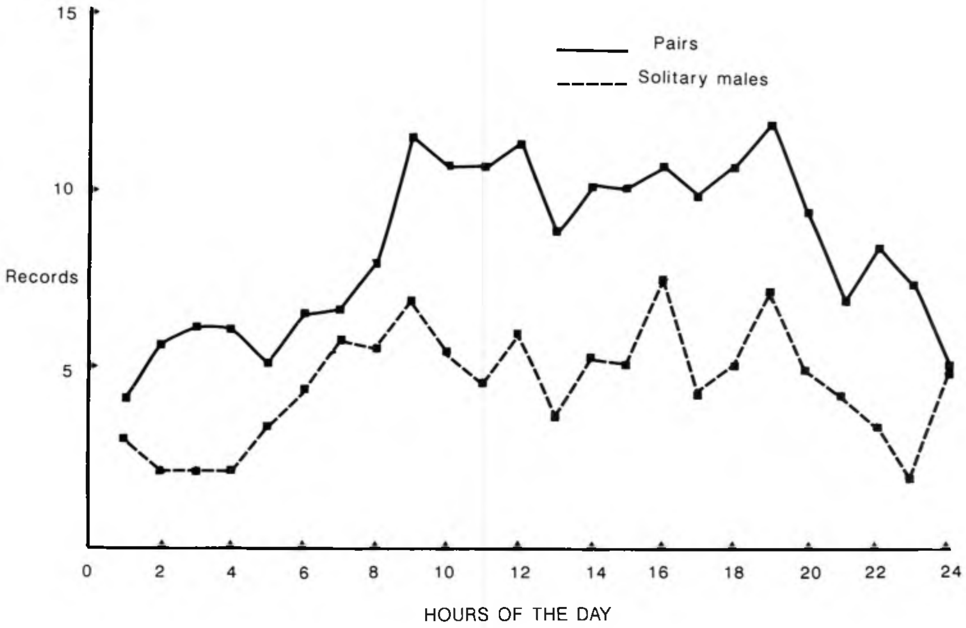

Figure 2. The mean numbers of Harlequin pairs and unpaired males on the study area at different times of the day.

Table 1. The percentage of the day spent in the various locomotory activities for the three class of Harlequin Duck. (Bars connect values not significantly different at the 0.01 level).

Activity	Status Paired female n = 1060	Paired male n = 1052	Unpaired male n = 500
Sitting	48.1	42.8	41.0
Standing	27.8	29.8	34.6
Walking	2.5	2.2	1.2
Swimming	21.0	25.5	22.6
Flying	0.6	0.5	0.6

Females sat significantly more than either category of male ($X_2^2 = 9.3$, $P<0.01$), and this was the only activity category that differed significantly between the three categories of duck. Flying was rare. When flying the Harlequin kept low over the water, following the bends in the river and preferring to fly around islands rather than over them. Flying often occurred at the end of intense agonistic interactions, particularly if these took place on land.

Figure 3 shows how the incidence of the major activity categories changed throughout the day for paired females, paired males and unpaired males. The pattern for each category of duck is similar. Following a peak of sitting around midnight, when most birds are apparently asleep (see below), there is a sharp drop over the next three hours. Sitting then stays at a low level until around 1300 h when it begins to increase slowly back to reach the high point at 2400 h. There is no evidence of a peak in resting between 0800 h and 1400 h as reported by Bengtson (1966). The incidence of swimming changes in the opposite fashion. There is a sharp increase in swimming after midnight which peaks around 0300 h and is followed by a slight decline. A further smaller rise in swimming occurs in the late morning and then, from around midday onwards, the incidence of swimming slowly declines to reach its lowest point around 2300 h.

Resting patterns

A bird was defined as 'resting' if it was standing or sitting in one of the following two postures. Harlequins in the *head-on-back* posture have the beak tucked under one of the wings on the back and in the *head-low* posture (see Fig. 4) the neck is not extended. Eye closure is most often seen in *head-on-back* birds. Ninety-five percent of all birds in the *head-on-back* posture were sitting compared with only 33% of ducks in the *head-low* posture.

Table 2 gives the mean percentage of the day spent resting by the three categories of duck. Paired males spent significantly less time resting than did either their mates or unpaired males ($X_2^2 = 11.0$, $P<0.005$). Resting females were more likely to adopt the *head-on-back* posture than were resting paired males or resting unpaired males (paired female = 66%, paired male = 51%, unpaired male = 50%, $X_2^2 = 36.2$, $P<0.001$). This finding does not result simply from the fact that females sit more than males since it is present also in sitting birds. Seventy-seven percent of sitting females were *head-on-back* compared with 69% for sitting paired males and 69% for sitting unpaired males ($X_2^2 = 8.9$, $P<0.02$). Figure 5 shows how the incidence of resting changed throughout the day. As the resting postures are most commonly shown by sitting birds it is not surprising that the

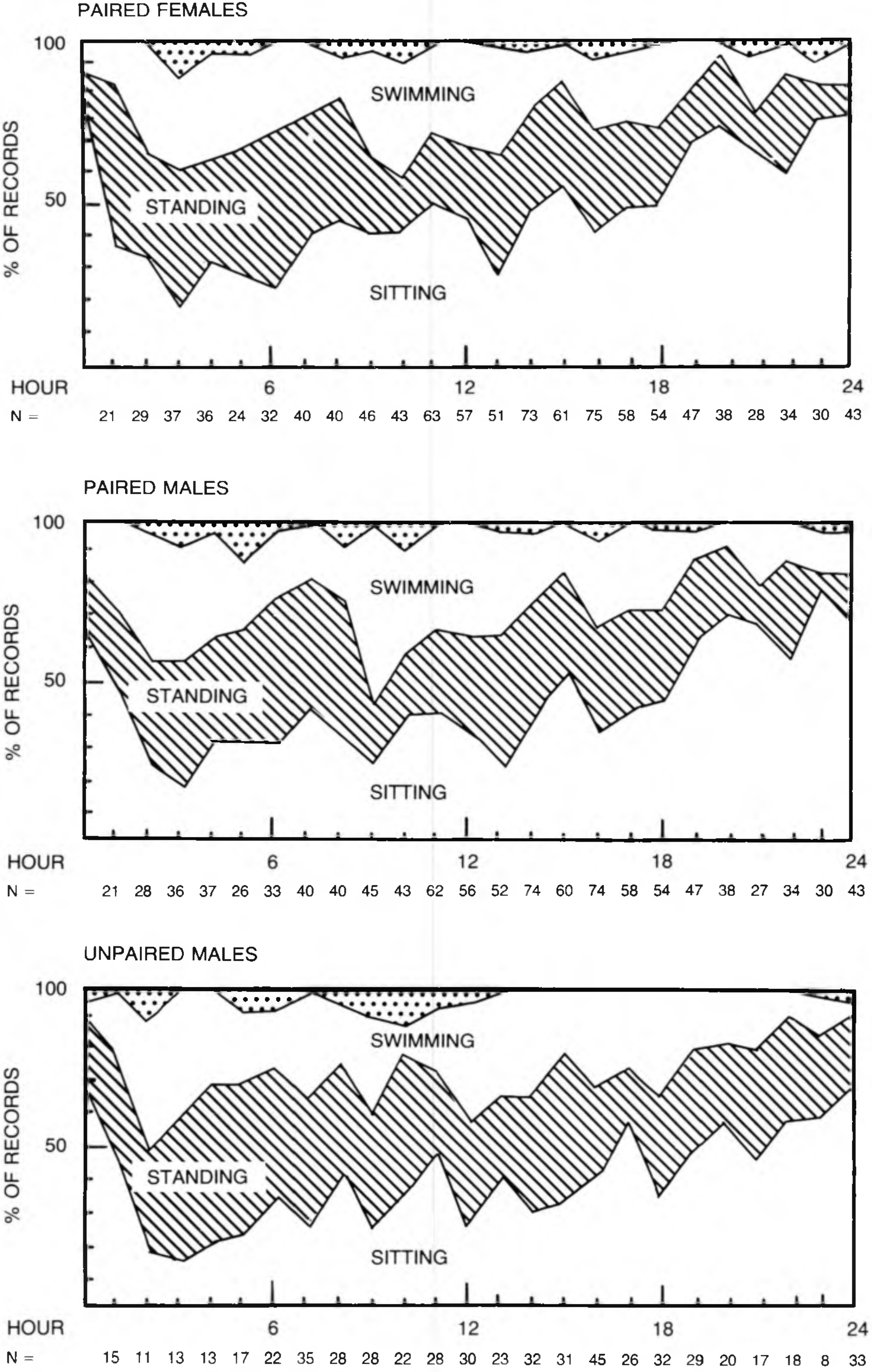

Figure 3. **The daily cycle of Harlequin activity.** The small shaded section at the top of each graph is made up of walking, running and flying (see Table 1).

Table 2. The percentage of the day spent in the major categories of behaviour for the three classes of Harlequin Duck. (Bars connect values not significantly different at the 0.01 level).

Behaviour Category		Status	
	Paired female $n = 1051$	Paired male $n = 1053$	Unpaired male $n = 571$
Resting	59.8	53.7	60.6
Preening	19.2	12.8	14.9
Feeding	7.6	7.1	7.0
Alert	5.0	5.5	7.7
Agonistic	2.7	5.4	1.8
Moving	5.7	15.5	8.0

Figure 4. A pair of Harlequins standing *head low*, **characteristically close to one another and the water.**

pattern of changes in resting behaviour closely follows that found in the incidence of sitting. There is a marked drop in the proportion of birds that are resting from a high at 2400 h to a low around 0300 h. Thereafter the resting proportion slowly and steadily increases back to the original level. The patterns for all categories of duck are similar.

Our category of 'alert' behaviour consisted of birds which were sitting, standing or walking in one of two postures. Harlequins in the *head up* posture have the neck extended upwards so that the head is raised

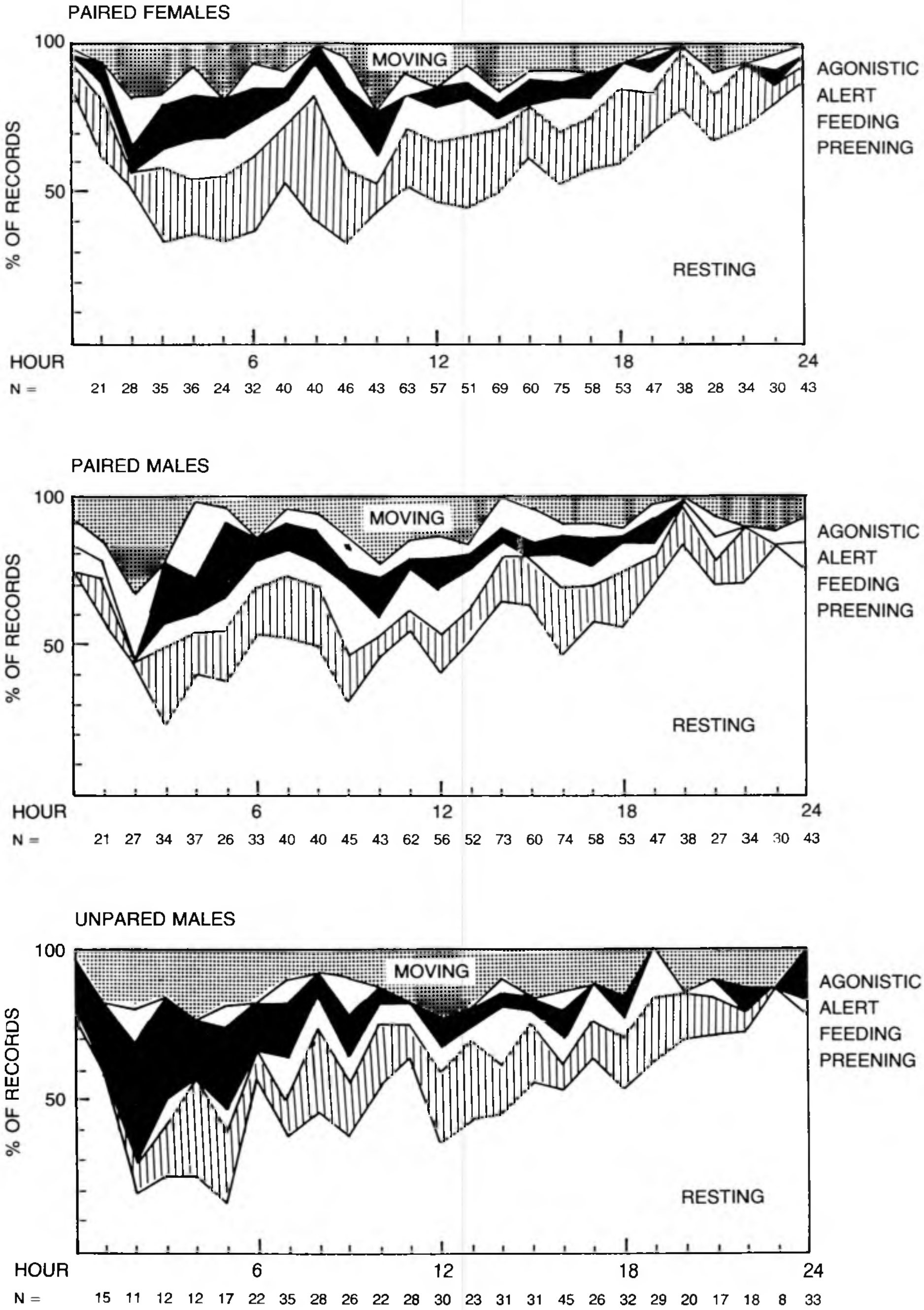

Figure 5. The daily cycle of the major categories of Harlequin behaviour (see text and Table 2).

some distance above the back (see the posture of the sitting female in Fig. 6). Ducks in the *extreme head up* posture have the body angled upwards and the neck extended to its full extent (as in the postures of the two males in Fig. 6). It was often difficult to judge the relative neck position of swimming birds and hence these have been excluded from the 'alert' category. Unpaired males spent the most time alert (Table 2).

Preening

A large proportion of the day was spent preening (see Table 2), perhaps because swimming and diving in cold and fast-flowing rivers necessitates frequent feather maintenance. Females preened significantly more often than males ($X^2_2 = 16.6$, $P<0.001$). Only 18% of preening occurred in the water where, even in many calmer stretches, the ducks had to paddle to maintain position. *Splash bathing*, in which the head, neck and back are repeatedly submerged under the water and the wings vigorously flapped, was obviously confined to water. The *upward stretch* was usually seen towards the end of a preening bout and involved rearing up, extending the neck and beating the wings between two and four times. Both of these behaviour patterns were common in the preening that followed copulation (see below). Preening was common throughout the day, falling to low levels between 2300 and 0200 h (see Fig. 5).

Feeding behaviour

The Harlequins fed mainly on the larvae and pupae of blackfly (especially *Simulium vittatum*), and to a lesser extent upon chironomids (Gudmundsson 1961, Bengtson & Ulfstrand 1971, Bengtson 1972), on the river bed. Birds in all three status categories spent relatively little time feeding and there were no significant differences between them (see Table 2). There was little diurnal variation in feeding activity apart from a drop around the hours of midnight, when Harlequin were most sedentary (see Figs. 3 and 5). This general picture contrasts with the findings of Bengtson (1966, 1972) who reported three peaks of diving activity at 0500–0800 h, 1700–2000 h and midnight.

The main method of gathering food was by diving. The mean dive duration of 264 dives of 31 birds was 10.7 s (± 2.3) and the

Figure 6. Agonistic encounter between two pairs of Harlequins. The female at the bottom is *head up* whilst the two males are performing *head nods* at each other.

maximum duration was 26 s. From a larger sample Bengtson (1966) obtained a mean dive time of about 16 s with one dive as long as 35 s. It is likely that dive duration will vary with locality as a result of variation in food availability and strength of current. By comparing the dive times of members of pairs diving together (thereby controlling for locality differences) it was found that females had a significantly higher average dive duration than their mates (female $\bar{x}$ = 11.6s ± 1.1, male $\bar{x}$ = 10.3s ± 1.0, $t_9 = 3.4$, $P<0.01$).

Harlequins dive with their wings open and appear to use them as they move around the river bottom. As Bengtson (1966) noted, they have an amazing ability even when diving in very fast 'white' water to emerge exactly in the same position as the original dive. On the basis of the amounts of time the ducks spent in calm, fast and white stretches of the Laxá we would expect, if they dived at random, 43% of dives in calm water, 51% in fast and 6% in 'white' water. The observed figures were 15% in calm, 76% in fast and 9% in 'white' water (n = 135). Clearly the ducks preferred the fast stretches (X^2_2 = 32.4, $P<0.001$), probably because larvae are less plentiful in the calmer, muddier regions of the river.

Food was also obtained by scraping larvae off rocks just under the surface of the water (12% of feeding records) but *up-ending*, as typically observed in dabbling ducks, was rare (1% of the feeding records). Bengtson (1966) noted a further feeding technique which involved skimming insects off the water surface. This behaviour became common later in the summer (after our study period) during the peak blackfly emergence period.

Agonistic interactions

Although there were preferred loafing sites, these were not defended and several pairs could often be seen sitting together at such places. Although there was no evidence that the birds formed territories, males stayed close to their mates (nearest neighbour distance for sitting birds = 0.9 m ± 0.3) and usually positioned themselves between the mate and the next nearest bird. Thus for pairs in which the mate is the first nearest neighbour, the mean distance to the second nearest neighbour (almost invariably the same individual for both members of the pair) was significantly greater for the female than for the male, as long as the female's second nearest neighbour was within about 6 m (Table 3). We interpret this to mean that mate guarding became a less pressing requirement for males when the nearest male was further away.

Males defended their mates against other Harlequins who came too close and often the females would enter into these interactions, a detailed analysis of which will be presented elsewhere (Lazarus, Inglis & Torrance in prep.). The *head nod* (Bengtson 1966) was the main agonistic display employed; it consists of an upward and forward movement of the head and neck through an elliptical trajectory (Fig. 7). There is much variation in the dimensions of the ellipse described by the head but the movement is directed forwards rather than to the side of the actor's body. In males the movement is typically smooth and the ellipse large; in females it is often jerky and the ellipse smaller, sometimes involving only movements of the head on a stiffly extended neck.

If the intruder failed to retreat in response to the initial display, the head nod movement became more vigorous with the long axis of the ellipse shifting more and more towards the horizontal. The orientation also changed so that the beak became clearly pointed at the intruder. Further persistence by the intruder sometimes resulted in an attack in which the initiator ran very fast with the neck extended and the beak open at the other bird(s) (the *extended neck* posture). When the *extended neck*

Table 3. Mean distance to nearest neighbour other than mate for members of Harlequin pairs.

	Mean distance in metres (±SE) Female	Male	
Distances < 3m	2.1(±0.06)	1.8(±0.06)	t_{255} = 7.0, P<0.001
Distances 3 m – 6 m	4.5(±0.09)	4.2(±0.09)	t_{240} = 4.1, P<0.001
Distances 6 m – 9 m	7.6(±1.20)	7.6(±1.10)	t_{179} = 1.3, NS

Figure 7. A male Harlequin performing a *head nod*: 3 frames per second, reading from top to bottom.

posture was used on the river, the initiator would half-swim, half-run, very fast over the water with the wings held close to the sides and the neck outstretched at the intruder (this is called the *rush*). In males the *head nod* and particularly the *extended neck* were accentuated from the receiver's point of view by the three white bands on head and flanks, which circle the beak as it is thrust towards the opponent. These, and other white patches on the male's plumage, acted surprisingly as camouflage; at a distance a male was rendered quite cryptic when swimming on rushing white water. During agonistic encounters individuals often became very vocal, uttering squeals and squeaks which appeared to become louder and more frequent the more intense the visual displays became. The influence of the *head nod* on the receiver's own agonistic behaviour varied with the orientation of the displaying bird, and with the sex and breeding status of the interactants (Lazarus, Inglis & Torrance in prep.).

Paired males spent 5.4% of their records *head nodding*, significantly more than both unpaired males and paired females ($X^2_2 = 18.5$, $P<0.001$, see Table 2). Females seldom initiated an agonistic encounter but they were seen to *incite* their mates against neighbours. In this behaviour the female extended her neck horizontally and bent it to point at the intruder before then turning her head and neck to point at her mate. This sequence of extending the neck first at the intruder and then towards her mate was often repeated several times. The female was also seen to *head nod* at her mate after extending her neck towards the intruder. Following inciting, the mate would usually *head nod* at or *rush* at the intruder. Bengtson (1966) observed similar inciting movements by females. When females became involved in agonistic interactions they were more likely to escalate into the *extended neck* display than were males (Lazarus, Inglis & Torrance in prep.).

Another type of head nod, the *forward head nod*, (Fig. 8) was also commonly observed in agonistic interactions. In this movement the neck is extended and moved backwards and forwards horizontally without the marked elliptical movement seen in

Figure 8. A male Harlequin performing a *forward head nod* **in the presence of a model of a female Harlequin:** 3 frames per second reading from top to bottom.

the *head nod*. The *forward head nod* was seen in many contexts (e.g. in copulation sequences, when close to other species of duck, before moving off) and was also observed in solitary birds. It may be indicative of a high level of excitement or anxiety (Lazarus, Inglis & Torrance in prep.).

Male Harlequins were observed threatening their mates, most commonly during a copulation sequence (see below), but also during agonistic interactions between pairs. In the latter context the male would usually run in the *extended neck* posture or *rush* towards his mate after having been attacked by another bird. This behaviour may function to ensure that the mate left the area with the defeated male.

As the presence of other species within the study area was rare it is not surprising that interspecific aggression was also seldom seen. Of the seven observations recorded in which Harlequins initiated agonistic encounters, five involved aggression against Mallards and the remainder against Barrow's Goldeneyes. In two of the encounters, both against solitary male Mallard, the other individual was actively chased away by the Harlequin but in the remaining instances the aggressive displays were apparently ignored by the other birds. There were many instances in which Barrow's Goldeneyes initiated agonistic encounters and in these cases the Harlequins were always chased away.

Copulation sequences

As copulation sequences were infrequent and generally brief, only two copulation records are present in the scan data. However, 49 copulation sequences were observed in which mounting was attempted. On the basis of these records, there was no obvious peak of copulatory activity during the day.

The most distinctive behaviour of the female during copulation sequences was the *prone* posture in which the female lay with her neck stretched out low over the water and her tail raised slightly. There were six records in which this posture was seen but no successful mounting resulted. In three of these records the courtship was disrupted by other Harlequin, in a further two records the female abruptly broke off and fled before the male could mount her, whilst in the last case the male appeared oblivious of his mate, who eventually gave up swimming in the prone posture and resumed feeding.

In 24 of the 49 copulation sequences the pair had been monitored for some time prior to the female assuming the *prone* position, and the mean time between the female going *prone* and the male mounting was 60.4±12.0s (n = 9). In eight (33%) of these records the female went *prone* after her mate had *rushed* at her but without the subsequent physical attack shown in an agonistic context. In a further six (25%) records the male directed a *head nod* at his mate who then went *prone*. Once a female is *prone* the most common male behaviour is to peck repeatedly at the back of her outstretched neck. In four (17%) of the records, however, this pecking immediately preceded the female going *prone*. In the remaining six records (25%) the female clearly initiated copulation by swimming *prone* in front of her mate.

In 13 records it was clear whether or not the cloacas of the copulating pair came into contact while the male was mounting the female. In the ten records where contact was made, no further mounts were attempted, whereas in the three records where contact was not made, subsequent mountings were observed ($P = 0.0035$, Fisher exact probability test). This result suggests that the male attempts to mount more than once only if he failed to transfer sperm on the first mount. Similarly the female remained *prone* only after apparently unsuccessful mountings.

The courtship sequence was divided into a pre-copulation period up to the first mounting, and a post-copulation period after the last mounting. Figure 9 gives the percentage of courtship records containing various male behaviours for both pre- and post-copulation sequences. One of the most common behaviours, seen only pre-copulation and in no other context, was the repeated pecking of the back of the female's neck. This could be a few gentle nibbles with the bill or a series of powerful pecks. The pecks were generally directed towards the part of the neck grasped by the male during mounting. The female did not respond to pecks at this area. However, when occasionally the male pecked her flank (possibly as a result of a misdirected aim at the neck), she most frequently pecked the male in return before resuming the *prone* posture. Another common male behaviour, rarely seen outside courtship, we termed the *upward shake*. In this movement the male throws his head a little way over his back before extending the neck forward and upward whilst raising his body out of the water. The wings are held close to the body which is then shaken briefly (sometimes accompanied by a tail shake) before settling back onto the water (see Fig. 10). The *upward shake* was more common

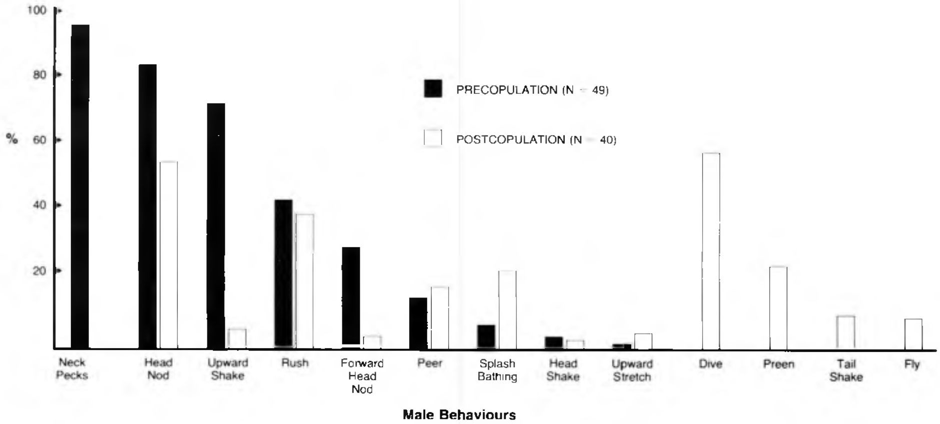

Figure 9. The percentage of copulation records containing various Harlequin male behaviours (see text for description).

in the pre-copulation sequence (see Fig. 9) and was given on only two occasions not in the presence of a *prone* female.

The other behaviours seen in both pre- and post-copulatory sequences were mostly components of preening (e.g. *splash bathing*, *upward stretch*) and of agonistic behaviour (e.g. *head nod*, *rush*). The behaviour called *peering* is, like the *forward head nod*, seen in many contexts; the duck swims with its head partially submerged and its beak held under the water (see Fig. 11). This may be a display, as Bengtson (1966) suggests, although it has no obvious effect upon the behaviour of neighbouring birds (Lazarus, Inglis & Torrance in prep.) and is also shown by solitary individuals.

Figure 10. A male Harlequin performing an *upward shake* **during a copulation sequence.**

Figure 11. A male Harlequin *peering* **and his mate swimming** *head low*.

Figure 12 gives the percentage of copulation records containing female behaviours for both pre- and post-copulation sequences. The most common behaviour, *prone*, appeared in no other context. As with the male, the other behaviours are also components of agonistic behaviour and preening. The behaviour *rush away* consists of half running over the water using the wings as paddles. It was often seen when a bird, usually a female, was trying to escape the harrassment of several males. Harlequins use a similar technique to move upstream over fast flowing water. *Rush away* differs from the *rush* shown in agonistic encounters, not only in that the direction of movement is away from the other bird rather than towards, but also in that the wings are used rather than held close to the body.

The most common pre- and post-copulation sequences, as derived from a transition analysis of the 49 records, are as follows. The male initiates most sequences by using the *head nod* and/or *rush* displays. The female then goes *prone* and generally stays in this posture until mounted. The male seldom mounts quickly but repeatedly pecks at the base of her neck, breaking off occasionally to *head nod* and *upward shake*; *forward head nods* are also shown at this time. High pitched 'squeaks' were heard frequently in the pre-copulation phase and appeared to be uttered only by the male. The male then mounts and usually grasps the back of his mate's neck in his bill, by which time the female is partially submerged. The male stays on the female for only a few seconds (during which time the cloacas of the pair may come into contact) before the female's body rotates, possibly as a result of the current, and the birds separate. Immediately after copulation the female would vigorously *tail shake*, *rush away* and then dive. The male usually *head nods* at his mate and dives when she does. After the dive both birds preen vigorously showing, in particular, *splash bathing* and *upward stretch* movements. Preening can continue for several minutes before the pair swim away. If the male does not let go of the female's neck immediately after coming off

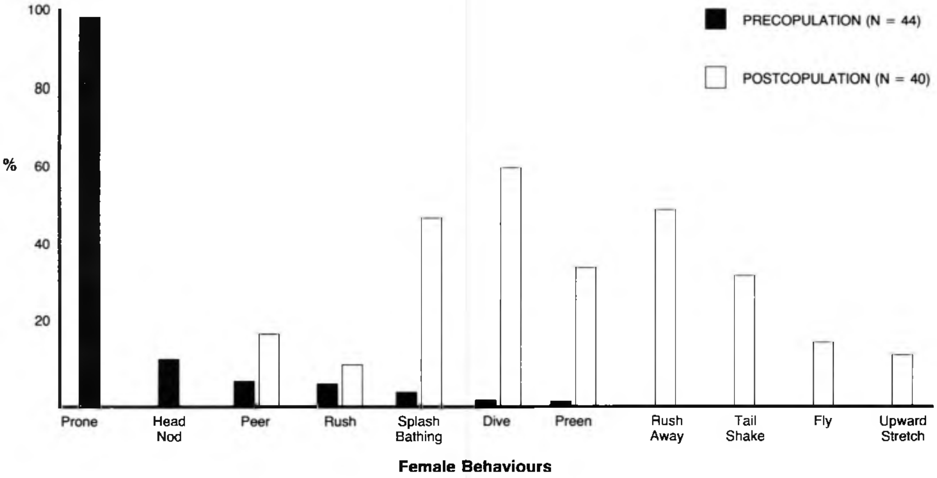

Figure 12. The percentage of copulation records containing various Harlequin female behaviours (see text for description).

her back, she will often *rush* at him and peck him vigorously. Similarly the male may *rush* at the female after she has surfaced from the dive. This usually results in the female taking flight followed by her mate.

Rare behaviour patterns

There were five observations of a behaviour we termed a *head throw*, in which the head was suddenly erected, the beak pointed into the air and the head thrown back so that the nape touched the bird's back. After a brief pause, the head was then returned to the normal position. All the movements were made by males, and in four of them we are certain that the bird called during the movement. Bretherton (1896) and Yeates (1951) have described a similar behaviour which resembles the *cooing-movement* (McKinney 1961) threat display of Eider Ducks *Somateria mollissima*. In three of the five observations the Harlequin *head throw* was given in the presence of people on the river bank and in another instance when a Barrow's Goldeneye was close by. It may therefore be an alarm response.

On three occasions female Harlequin were observed showing a behaviour which we called *hovering*. The female reared up into an *upward stretch* but instead of flapping her wings only a few times they were beaten very rapidly for about 5 s so that the bird seemed to be almost hovering. At the same time the female would utter a series of very fast high-pitched squeaks. In all three cases the female had been making small jerky *head nods* with the neck extended before *hovering* and in two of the instances the female resumed these *head nods* after the *hovering* had ceased. In each case the female and her mate were involved in agonistic interactions with another pair.

The *chin lift* consisted of a rapid raising and lowering of the head from the horizontal. On three occasions females used this posture as an inciting display and directed it at an intruding male; whilst in the one other, observation the *chin lift* was directed at the mate, seemingly in the absence of other birds. In the eider the *chin lift* is only shown by females and is used either as an inciting movement or after copulation (McKinney 1961).

Two aerial chases were observed on the same day, 22 June, 100 minutes apart. We concluded that these were chases since they were our first observations of birds flying more than a metre or two above the water and not in close unison. In the first observation a male chased a female in the air and then over the water and on land (and briefly a third bird joined them, sex unknown), *head nodded* at her on land and, while on the water, pecked her on the back of the neck and mounted her without her assuming the *prone* posture (the only observation of copulation without *prone*). Once mounted, the female did not struggle. We classify this as a 'forced copulation attempt' or 'forced pair copulation attempt' (McKinney *et al.* 1983), at a time when the female was either laying or had already completed her clutch (pers. obs., Bengtson 1972). The second observation involved a pair, but it was not possible to see who was chasing whom. When these observations were made few Harlequin were to be seen on the river; females were incubating and males were gathered in groups before leaving for the sea. Consequently these chases might have involved a female away from the nest on a feeding trip and a strange male, rather than an established pair.

Discussion

Time budgets, agonistic behaviour and reproductive strategies

The reproductive priority of paired males in the pre-nesting period (apart from copulation) was mate guarding, the close following of the female partner by her mate (Birkhead *et al.* 1987). Mate guarding functions to prevent fertilization by other males and to allow the female undisturbed feeding at a time when she is forming eggs (McKinney 1986). Mate guarding is strongly developed in dabbling ducks (McKinney 1986) and evidence for it in the Harlequin was clear. Paired males, although not territorial in this population, stayed near their mates at all times, keeping between the female and other males when resting with neighbours on land, and attacking both pairs and unpaired males that came too close, both on land and water. When neighbours were beyond 6 m, resting paired males no longer significantly placed themselves between partners and their neighbours, probably because if an approaching male is more distant there is ample time to intervene between the partner and the intruder.

It might be predicted that paired males would spend more time vigilant than unpaired males, since vigilance could serve a mate guarding function. Alternatively vigilance might be equally beneficial for unpaired males because of the opportunity it might afford for an unseen approach to a female. The data show that the two types of male spent a similar proportion of time both in the potentially vigilant *head up* posture and in the non-vigilant *head-on-back* posture.

However, these predictions probably overestimate the value of vigilance in this context, since an intruding male could not copulate with a female unseen by her mate. Females were never seen out of sight of their males (the habitat being very open), or more than a few metres from them, and were never seen attempting to leave their mates (except perhaps in the two chases described). Additionally, pairs and unpaired males that approached a pair were threatened by the paired male (and sometimes by the female too) and, in the hundreds of such encounters that we observed, in some 300 person-hours of observation in a completely open habitat, a female was never seen to leave with a strange male or to be mounted by one. The differences between paired and unpaired males that probably do reflect an increased burden associated with mate guarding are the smaller proportion of time spent resting (more time walking and swimming) and the greater proportion of time spent in agonistic behaviour by paired males. It might be expected that the reproductive priority of unpaired males would be to copulate with paired females (unpaired females being very rare). However, they never succeeded in this and spent little time in attempting it (agonistic behaviour, Table 2, reflecting approaches to pairs). This can not be because they were not sexually interested in females since they spent a great deal of time near, and showed pre-copulation behaviour towards, fibreglass models of 'unpaired' females (Lazarus, Inglis & Torrance in prep.). Unpaired males might be young birds or birds of low quality (only a very few were immature); which may be why they had not obtained a mate in the first place, due to female choice or male-male competition. If so, they may have had little chance of winning an encounter with a guarding male (and his female) and consequently expended little effort in attempting to.

Extra-pair copulation by paired males has been increasingly observed in monogamous bird species (Ford 1983, Birkhead 1988) but was absent in the Harlequin (apart from one possible case after an aerial chase). This contrasts with the dabbling ducks, in which paired males exhibit forced extra-pair copulation, but also show mate guarding (McKinney *et al.* 1983, McKinney 1986). Mate guarding and extra-pair copulation are behaviourally incompatible mating strategies (McKinney 1986), and must be traded off against one another as alternative methods of producing offspring. The combination of the two strategies varies between species within the Anatidae, the Harlequin opting for an extreme combination of continuous mate guarding (giving a high certainty of paternity) with little or no extra-pair copulation.

Gauthier (1988) offers an explanation for this interspecific variability in terms of variance in habitat stability and, although the Harlequin fits his model, it still leaves a good deal of the variability unaccounted for. Another possible factor is bird density, a higher density increasing the chance of cuckoldry for a male when he leaves his mate to seek an extra-pair copulation himself, and decreasing his chance of success in extra-pair copulation due to greater competition with other males. High density should thus select for mate guarding rather than extra-pair copulation. Our study population has been recorded as having by far the highest density of any studied in Iceland from 1965 to 1971 (Bengtson 1972) and during our study contained a mean of 10.5 pairs and 6.0 unpaired males on 418 m of river, figures comparable to those recorded earlier.

The female's reproductive priority before nesting is to feed efficiently in order to produce eggs and to prepare herself for incubating, which she completes unaided. The females spent no more time feeding than either paired or unpaired males, perhaps because the high density of food in our study area (see below) meant that food requirements could be readily met without compromising other components of the time budget. However, females dived for longer than their mates, perhaps seeking more nutritious prey items. Females may have conserved more of the energy gained from food than males since they spent more time sitting (and more of their sitting time in the sleeping *head-on-back* posture). Conversely, however, they spent more time (and presumably more energy) than males in preening, either because they dived for longer or because males were sacrificing the benefits of preening as a result of other demands on their time (although no single alternative demand is apparent in the time budget).

How does selection act on the female in relation to extra-pair copulation? If she leaves her mate altogether to form a new pair-bond she is likely to be gaining a new mate who is more likely to desert her, due to his uncertainty of paternity, since she may already be carrying a fertilized egg or sperm from her first mate. Only if the takeover is too early in the season for sperm from the first mate to be used for fertilization would a second mate be no more highly selected to desert than a first. In addition, rejecting the attention of unpaired males is adaptive if such males have heritable traits of inferior quality. On the other hand, females might gain from extra-pair copulation by increasing offspring variability, or by mating with a fitter male (Moller 1988, Smith 1988), although the latter effect is potentially greater where males contribute parental care to the young in addition to genes. Since females stayed close to their mates and showed no signs of soliciting extra-pair copulation it could be inferred that selection did not favour extra-pair copulation in females. However, if females did favour extra-pair copulation it would be almost impossible to hide it from their mates, since visibility on the water is so great. They would then be at risk from forced pair copulation (Birkhead *et al.* 1987) from the mate which would render their infidelity largely ineffective. Consequently females might favour extra-pair fertilization but be unable to achieve it and therefore selected not to pursue it. However, since females incited their mates to attack, and themselves threatened, both pairs and unpaired males, they were clearly actively avoiding male advances, either because extra-pair copulation is disadvantageous to them or because of the costs of interrupted feeding.

Comparisons with other fast-water ducks

The fast flowing mountain streams preferred by the Blue Duck, Salvadori's Duck, Torrent Duck and Harlequin Duck are similar in physical conditions and invertebrate fauna through the world (Hynes 1970). It is not surprising therefore that these species are behaviourally alike in several respects. They fly low over the water surface following the meanderings of the streams rather than cutting across land. They are very agile at running over wet rocks. They are superb swimmers and expert divers, searching underwater for aquatic insect larvae. The Harlequin and Torrent Ducks have longer average dive times (x̄ Harlequin Duck = 16 s, Bengtson 1966; x̄ Torrent Duck = 16 s, Johnsgard 1966) than the other species (x̄ Salvadori's Duck = 12 s, Kear 1975; x̄ Blue Duck = 11 s, Kear & Burton 1971), which place greater emphasis on food gathering by *up-ending* (Bell 1969, Eldridge 1986b). The Harlequin, Torrent and Blue Ducks spend approximately the same percentage of the day preening (Eldridge 1986a,b) and all species use high-pitched vocalizations which can be heard above the low frequency noise of the rushing water.

However, the behaviour of the Harlequin Duck on our study area differed from that of the other species in two major respects. First, only 7% of the day was spent feeding, which is well below that for the other ducks. Eldridge (1986b) reported that a pair of Blue Duck spent approximately half the observation time feeding; whilst this proportion for three pairs of Torrent Ducks (Eldridge 1986a) varied between 17% and 38%. Second, all the other species are strongly territorial whilst the Harlequins in our study defended only their mates. In these two respects our results may be atypical and result from the high food availability in the Laxá. This allows a density of Harlequins far greater than on other Icelandic rivers (Bengtson 1966, 1972). It has been reported (Darcus in Myers 1959, Bengtson 1966) that where Harlequins are at much lower densities, presumably as a result of lower food availability, each pair does indeed defend a stretch of river for at least part of the breeding season.

Unfortunately little is known of the displays of Salvadori's Duck but it is possible to compare the repertoires of the other species. The Blue Duck has several displays that resemble aspects of Harlequin behaviour. The *head-bob* of the Blue Duck (Eldridge 1985) resembles the Harlequin *head nod* except that the former is also accompanied by an elevated tail and lifted primary feathers. Scott (1958) describes a jerky back-and-forward movement of the head that Blue Ducks "make in the presence of man" which appears similar to the Harlequin *forward head nod*. Both species use an *extended neck* display in agonistic encounters and the Harlequin *rush* appears to be identical to the Blue Duck's *head low rush* (Eldridge 1985). The Blue Duck also exhibits a behaviour which, although not used for feeding, Eldridge (1985) has called *siphon-feeding*. A territorial bird, usually following an intruder, holds its neck and head outstretched low over the water and moves the lower mandible under the surface spraying water from commissures on either side. Apart from the water-spraying component this behaviour resembles *peering* in the Harlequin.

The Torrent Duck also exhibits a display similar to the *forward head nod* called *pointing*. It is shown in a wide variety of contexts and is exhibited "by seemingly wary birds" (Eldridge 1979). The *wing-flap* display of the Torrent Duck (Eldridge 1979) is identical to the Harlequin *upward stretch* and the *vertical shake* display (Eldridge 1979) prior to copulation resembles the Harlequin *upward shake*. However, the Torrent Duck has a number of aggressive displays without equivalents in the other species; i.e. the *mule-kick* (Scott 1954), the *body-bend* (Phillips 1953) and *barging* (Eldridge 1979).

The niche occupied by these species influences the nature of the displays in at least two ways. First, the level and nature of background noise from the rushing water reduces the importance of vocal communication and shapes the high frequency 'whistles' that are used. Second, the speed of the water prevents performance of elaborate displays of the sort shown by lake dwelling ducks. However, the fact that the Torrent Duck has a number of unique (but brief) displays suggests that some flexibility is possible even within these environmental constraints. Clearly more data are required on the types of displays shown by Harlequins at sea prior to their movement onto the breeding areas.

"Of all aspects of behaviour, none is more uniform within taxonomic groups and more indicative of evolutionary relationships than that associated with copulation" (Johnsgard 1966: 73). Many of the copulatory displays of the Harlequin Duck are also shown by other members of the Mergini (see Johnsgard 1965, Cramp & Simmons 1977). Rotatory *head-pumping* similar to the *head nod* is shown by the Bufflehead Duck *Bucephala albeola* and the goldeneyes *B. clangula* and *B. islandica*. Goldeneye males *rush* at the female prior to copulation, as do Hooded Mergansers *Mergus cucullactus*. The *upward shake* display is common to several Mergini and many plunge bathe after copulation. The most conspicuous behaviour seen in copulation in the Harlequin Duck is, however, not found in any other member of the Mergini. Only the Harlequin male repeatedly pecks the back of his mate's neck prior to mounting. This behaviour is reminiscent of that shown in the same circumstances by the Wood Duck *Aix sponsa* (Johnsgard 1965) and the African Black Duck *Anas sparsa* (Johnsgard 1965, McKinney *et al.* 1978). Kear & Steel (1971) observed that Blue Duck males occasionally pecked their mates repeatedly on the back and that this "might be the first stage of attempted mounting (although it was never seen to be followed by copulation)". Johnsgard (1965) and Kear (1972) have argued that the Blue Duck may have evolved from an ancestor, resembling *Anas sparsa*, that was the link between the perching and dabbling ducks. It is possible that the Harlequin Duck split off from a more primitive ancestor within the Cairini that resembles *Aix sponsa.* If this is the case then the neck pecking shown prior to mounting may be a true primitive character rather than an aberrant curiosity.

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