Activity patterns, diet, and feeding efficiency of Harlequin Ducks breeding in northern Labrador

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Abstract: The lack of data on summer diet and feeding behaviour for the endangered eastern North American population of Harlequin Ducks (*Histrionicus histrionicus*) prompted a study of activity patterns and feeding ecology in a coastal stream in Hebron Fiord, Labrador. Diurnal activity patterns varied by habitat and changed through the season. Extensive feeding occurred in slow-moving waters, contrary to expectation. Females spent 40% of daylight hours feeding during the prelaying period, more than twice the time spent by males and higher than that reported in other studies. Diurnal feeding patterns showed little variation in the prelaying period and major peaks of activity in the morning and evening during incubation and brood rearing. Larval Simuliidae (Diptera) were absent from a fecal sample taken in July but dominated the prey remains in feces collected in August. Dive times averaged 10–24 s and varied with depth of water. Dive–pause ratios of 1.7–2.2 were lower than previously reported. The results support the hypothesis that populations are food-limited on the breeding grounds, and suggest that there may be greater energy constraints on foraging effort in river specialists than in dabbling or other diving waterfowl.

Résumé : La rareté des données sur le régime et le comportement alimentaires d'été chez la population menacée de l'Arlequin plongeur (*Histrionicus histrionicus*) de l'est nord-américain a donné lieu à une étude de l'activité et de l'écologie alimentaires dans un ruisseau côtier du fjord d'Hebron, Labrador. L'activité diurne variait en fonction de l'habitat et a fluctué durant toute la saison. Étonnamment, les canards se sont alimentés abondamment dans les eaux lentes. Les femelles ont passé 40% des heures d'éclairement à se nourrir avant la période de pré-ponte, plus de deux fois plus longtemps que les mâles et plus longtemps que la durée signalée dans les autres études. L'alimentation pendant la journée subissait peu de variations au cours de la période de pré-ponte et deux périodes principales d'activité alimentaire ont été observées, le matin et le soir, durant l'incubation et l'élevage des couvées. Les larves de diptères simuliidés se sont avérées absentes d'un échantillon de fèces prélevé en juillet, mais constituaient les proies principales dans les fèces récoltées en août. La durée des plongées variait de 10 à 24 s en moyenne selon la profondeur de l'eau. Les rapports plongée–pause évalués à 1,7–2,2 ont été inférieurs aux valeurs mesurées au cours d'études précédentes. Les résultats appuient l'hypothèse selon laquelle les populations sont régies par la nourriture sur les territoires de reproduction et indiquent qu'il peut s'exercer sur l'effort de quête de nourriture des contraintes énergétiques plus importantes chez les spécialistes des eaux courantes que chez les canards barboteurs ou chez les autres oiseaux plongeurs. [Traduit par la Rédaction]

Introduction

Harlequin Ducks (*Histrionicus histrionicus*) nest primarily on swift-flowing streams (Bengtson 1966, 1972; Kuchel 1977; Dzinbal 1982; Wallen 1987; Inglis et al. 1989; Cassirer and Groves 1991; Rodway et al. 1998), where they feed on benthic invertebrates by diving, skimming, and upending (Bengtson 1966, 1972). A few studies of feeding ecology have been conducted in Iceland (Bengtson 1966, 1972; Bengtson and Ulfstrand 1971; Inglis et al. 1989), Montana (Wallen 1987), and Alaska (Dzinbal 1982; Dzinbal and Jarvis 1984).

The breeding ecology of the endangered eastern North American population of Harlequin Ducks (Goudie 1991) is poorly known and data on summer diet and feeding behaviour for this population are lacking. Food availability on the breeding grounds may limit populations (Bengtson and Ulfstrand 1971; Bengtson 1972), and greater understanding of food requirements and activity budgets is vital to recovery plans (Montevecchi et al. 1995). I investigated the feeding ecology of Harlequin Ducks on a coastal stream in northern Labrador, an area thought to support a substantial proportion of the eastern North American breeding population (Goudie 1991). The objectives of the study were to (*i*) determine activity patterns through a breeding season, especially the proportion of time spent foraging; (*ii*) relate foraging effort to reproductive status and sex; (*iii*) measure dive–pause ratios to obtain an estimate of feeding efficiency; and (*iv*) obtain information on diet.

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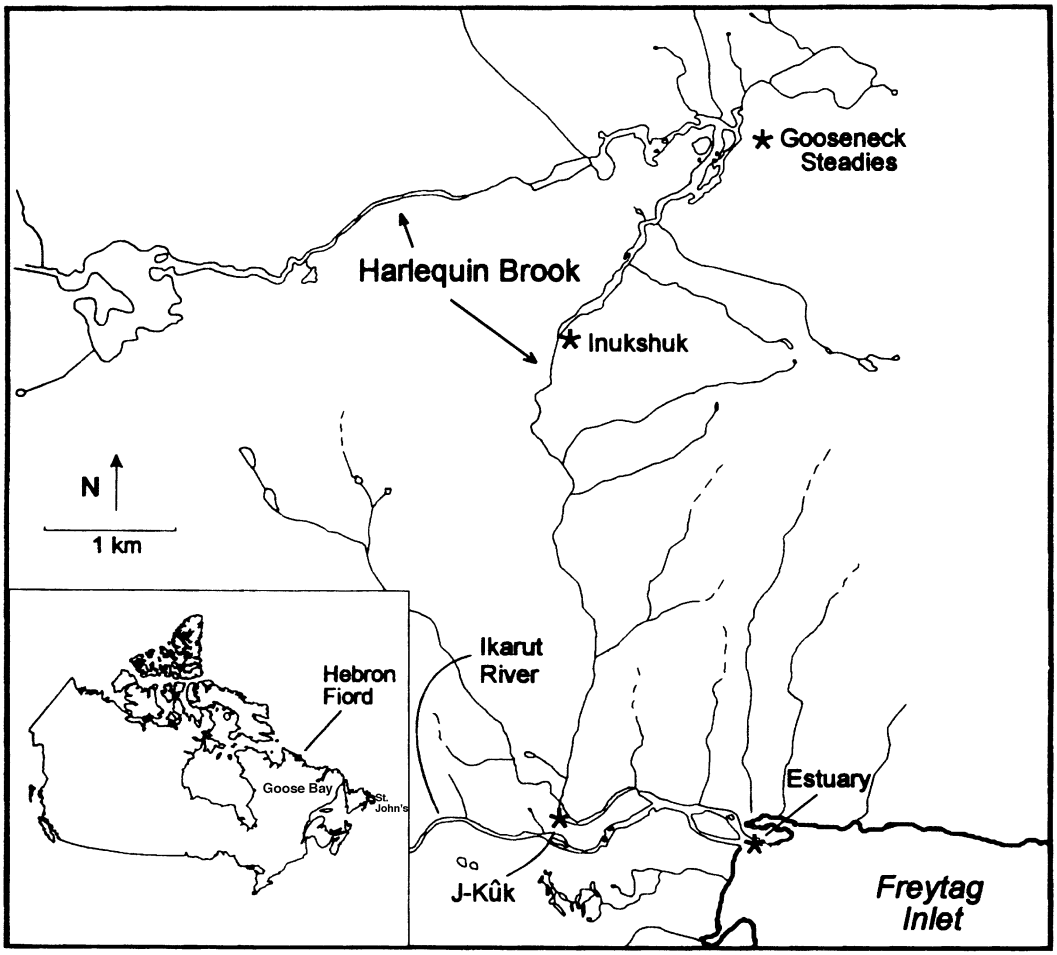
Methods

The study was conducted from 8 June to 14 August 1996 on an unnamed stream (Harlequin Brook; 58°09′40″N, 63°04′45″W), a tributary of the Ikarut River in the northwestern arm of Hebron Fiord, Labrador (Fig. 1). Coastal tundra habitat in the area rises to 400–700 m, with dense, shrub-covered sections along stream banks and on islands.

Four observation stations were established at 0 (estuary), 1.7

Fig. 1. Locations of study site and observation stations on Harlequin Brook, Hebron Fiord, Labrador, in 1996.



(J-Kûk), 6.0 (Inukshuk), and 8.3 km (Gooseneck Steadies) from the estuary at sites that were known to be frequented by Harlequin Ducks (Fig. 1). Stations were placed at vantage points above the river, except at the estuary where the station was on a broad sandbar, providing views of as much of the river as possible (about 500 m, on average). Depth and flow rate were 1–2 m and 1.0 m/s, 0.5–1.5 m and 0.6 m/s, <0.5 m and 1.8 m/s, and 0.5–2.0 m and <0.2 m/s over a substrate of pebbles, pebbles, boulders, and silt at the four stations, respectively. There was little shoreline vegetation at the estuary, sparse shrub cover at Inukshuk, and dense, overhanging shrubs at J-Kûk and Gooseneck Steadies. There were islands at Inukshuk and Gooseneck Steadies. J-Kûk was just downstream from a cluster of shrub-covered islands where Harlequin Ducks were known to nest (Rodway et al. 1998). Gooseneck Steadies is a meandering lake-like area with small, rapidly flowing feeder streams entering from the north and northwest. Ice and snow covered much of the shoreline and overhung sections of the brook at all stations during the first observation period.

Diurnal activity patterns were determined during the prelaying to early laying (16–21 June, 03:00–24:00; hereafter called prelaying), incubation (15–20 July, 04:00–23:00), and early brood-rearing periods (2–6 August, 04:30–22:30). Four-hour observation sessions were staggered over 3–4 days so that combined time blocks were representative of a full daylight period at each observation station. Additional observations were made from 02:00 to 03:00 and 23:00 to 23:30 on 17 June, from 03:00 to 04:00 on 16 July, and from 04:00 to 04:30 on 3–4 August to check for possible night feeding.

Behaviour was determined by means of instantaneous scan-sampling of focal groups at 30-s intervals (Altmann 1974). Groups of 1–4 birds (chosen or, often, the only birds present) were followed throughout the time they were visible from the observation post. Pairs were chosen during the prelaying period in order to compare male and female behaviour. Birds were considered present if they were out of sight behind islands or rocks but were known to be in the area, therefore numbers of observations do not always correspond to the percentage of time birds were present (see Tables 1 and 2). "Total number of birds × hours" is the number of birds multiplied by the length of time they were present during an observation period.

Feeding behaviours were categorized as diving, skimming, and upending (Bengtson 1972). Diving included time spent on the surface as well as under water unless the interval between dives was longer than 30 s, which is close to the maximum recorded dive time for Harlequin Ducks (Bengtson 1966, 1972; Inglis et al. 1989; see Results). Intervals longer than 30 s were coded as swimming. Dive–pause ratios were used to calculate time spent under water to allow comparisons with other studies. Dive and pause times were determined by recording to the nearest second when birds dove and resurfaced. Skimming refers to picking drifting prey from off or just under the surface or from stream banks, as well as scraping prey off shallow rocks without submerging. Putting the head under water and peering towards the bottom ("looking") and swimming were not considered feeding behaviours. Other behaviours are described in Bengtson (1966) and Inglis et al. (1989), using terminology from Myers (1959).

Table 1. Relative use by Harlequin Ducks of four observation areas on Harlequin Brook, Labrador, during dawn-to-dusk observations from 03:00 to 24:00, 04:00 to 23:00, and 04:30 to 22:30 in the prelaying to early laying, incubation, and brood-rearing period, respectively, in 1966.

	Estuary	J-Kûk	Inkshuk	Gooseneck Steadies
Prelaying to early laying period				
Percentage of time present				
Males	5.1	70.3	4.2	65.0
Females	5.4	71.9	4.2	71.9
No. of birds × hours				
Males	1.2	37.7	0.9	13.7
Females	1.2	50.7	0.9	39.7
Incubation period (females)				
Percentage of time present	3.1	20.5	71.7	17.9
No. of bird × hours	0.7	9.3	40.4	6.8
Brood-rearing period				
Percentage of time present				
Parent females	0.0	5.6	47.6	48.0
Chicks	0.0	5.6	47.6	48.0
Nonbreeding females	6.4	15.0	97.6	0.0
No. of bird × hours				
Parent females	0.0	1.0	8.4	8.6
Chicks	0.0	3.0	51.3	51.8
Nonbreeding females	2.2	5.1	38.4	0.0

Diet was determined from fecal samples collected on 4 August from a roosting site used for much of the previous 3 days by 4 failed or nonbreeding females at the Inukshuk observation area. An additional fecal sample collected from a mist-netted female on 3 July below the J-Kûk observation post gave an indication of diet earlier in the season. Insect parts from feces were sorted and identified to family for Diptera and to order for other taxa, using Pennak (1953) and Lehmkuhl (1979). Importance of each prey type is presented as a numerical proportion, which tends to underestimate the relative biomass of larger prey.

Non-independent, sequential observations of behaviour and dive and pause times were not appropriate for statistical analyses. As it was not possible to choose individuals randomly for observations, owing to the small numbers of birds present, I randomly picked 10% of total observations to use in statistical comparisons. Chi-squared tests were used to compare proportions of randomly chosen observations classed as feeding among groups. Dive and pause times were averaged for each diving bout by an individual, and one-way ANOVA was used to compare means of average dive and pause times among birds differing in reproductive status and sex.

Results

Activity patterns

Diurnal activity patterns varied by habitat and changed through the season. Most activity occurred at J-Kûk and Gooseneck Steadies during the prelaying period, at Inukshuk during the incubation period, and at Inukshuk and Gooseneck Steadies during the brood-rearing period (Table 1). J-Kûk was used as a loafing area by a "club" (Bengtson 1966) of up to 6 males and 10 females that spent most of their time resting and swimming. Groups of up to 5 nonbreeding or failed (hereafter, nonbreeding) females regularly roosted on the edge of the largest shrub-covered island at Inukshuk during the incubation and brood-rearing periods. Most feeding occurred at Inukshuk and Gooseneck Steadies. Little use was made of the estuary throughout the season. The main activities there were swimming and flying, birds being often in transit between the higher brook and offshore in the fiord.

Females spent more time feeding than males during the prelaying period ($\chi^2_1 = 27.4$, $P < 0.001$) and spent more time feeding in the prelaying than in the incubation ($\chi^2_1 = 71.8$, $P < 0.001$) and brood-rearing periods ($\chi^2_1 = 35.2$, $P < 0.001$; Table 2). Females during incubation and with accompanying broods had the lowest and similar feeding rates ($\chi^2_1 = 2.73$, $P = 0.098$) and chicks the highest (though not significantly higher than prelaying females; $\chi^2_1 = 1.18$, $P = 0.227$). Females without broods spent more time feeding than those with broods ($\chi^2_1 = 10.34$, $P = 0.001$). Aggressive and courtship behaviours occurred primarily during the prelaying period (Table 2). Aggressive encounters were observed during the brood-rearing period as females attending broods chased off closely approaching nonbreeding females. Alert behaviour by females was most frequent during the brood-rearing period.

Diurnal feeding patterns also changed through the season. Males and females in the prelaying period fed through most daylight hours, with no obvious peaks (Fig. 2). Females during the incubation period and females with broods fed mostly in the morning and evening. Nonbreeding females fed more through the middle of the day during the brood-rearing period (Fig. 2). Birds were not seen feeding when it was dark at the beginning or end of diurnal observation periods, and no evidence of feeding was observed during nocturnal observations. Harlequin Ducks were sighted flying and swimming by the

Table 2. Comparison of time budgets of Harlequin Ducks in the prelaying to early laying, incubation, and brood-rearing periods on Harlequin Brook, Labrador, in 1996.

	Prelaying period		Incubation period	Brood-rearing period		
	Males	Females	Females	Parent females	Chicks	Nonbreeding females
No. of observations	2857	2973	2172	1235	6588	1647
Percentage of total activity						
Feeding						
Diving	14.3	32.3	15.6	8.8	22.9	21.8
Skimming	2.2	7.3	1.3	7.3	21.5	3.6
Upending	0	<0.1	0.1	0	0.1	0
Total	16.5	39.6	17.0	16.1	44.5	25.4
Locomotion						
Looking	0.8	0.1	0.5	0.2	0	0.2
Swimming	28.9	18.6	24.3	34.0	18.6	21.9
Running	0	0	0	0.2	0.4	0
Walking	0.4	0.3	0	0.1	1.5	<0.1
Flying	0.8	0.5	1.0	0	0	0.1
Total	30.9	19.5	25.8	34.5	20.5	22.2
Social interaction						
Chasing	0.5	<0.1	0	0.1	0	0
Fleeing	0	0.2	0	0	0	<0.1
Head-nodding	2.3	1.5	0.8	0	0	0.1
Total	2.8	1.7	0.8	0.1	0	0.1
Maintainance						
Alert	0.6	0.2	4.0	9.9	0	1.0
Preening	4.6	4.6	0.8	3.0	2.7	4.2
Resting	44.6	34.4	51.7	36.4	32.4	47.1
Total	49.8	39.2	56.5	49.3	35.1	52.3

Note: Data are weighted by the number of birds and the percentage of time they were present at each of the four stations in order to calculate overall percentages (see Table 1).

estuary and J-Kûk observation posts at 02:00 on 17 June and 03:20 on 17 July.

Feeding efficiency

Most diving was observed at Gooseneck Steadies during the prelaying period and at Inukshuk during the incubation period. Samples of dive times from paired males and females and from unpaired females at Gooseneck Steadies during the prelaying period (Table 3) showed significant differences in dive times ($F_{[2,114]} = 4.55$, $P = 0.013$) and pause times ($F_{[2,85]} = 3.73$, $P = 0.028$), but not in dive–pause ratios ($F_{[2,85]} = 0.90$, $P = 0.410$). Unpaired females made longer dives than paired females (Tukey's test, $P = 0.009$) or paired males ($P = 0.041$), and took longer pauses than paired females ($P = 0.041$) but not paired males ($P = 0.634$).

In the shallower water at Inukshuk, dives of females were shorter ($F_{[2,96]} = 20.6$, $P < 0.001$) during the incubation period than, and dive–pause ratios were similar to ($F_{[2,68]} = 0.28$, $P = 0.757$), all those recorded at Gooseneck Steadies during the prelaying period and at J-Kûk during the brood-rearing period (Tukey's test, $P_s < 0.001$; Table 3, Fig. 3). Maximum dive times were 35, 21, and 34 s at Gooseneck Steadies, Inukshuk, and J-Kûk, respectively.

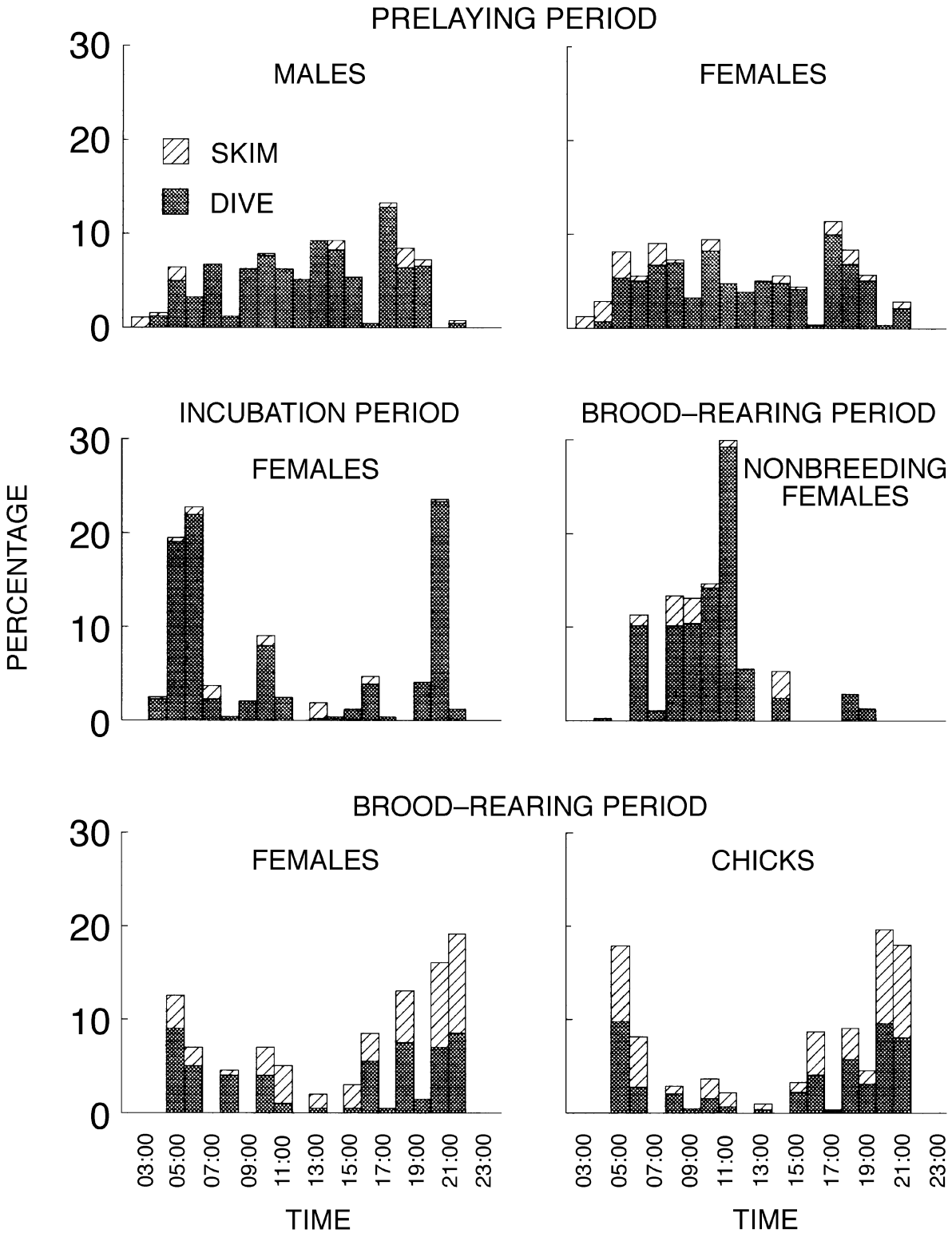
Diet

Simuliidae constituted 98% of remains found in feces collected on 4 August (Table 4). No simuliids were present and Trichoptera larvae were the most common prey item in feces collected on 3 July.

Discussion

Females spent 40% of daylight hours feeding during the prelaying period at Harlequin Brook, more than twice the time spent by males and higher than that reported in other studies. Prelaying females fed for 21% (including only time spent under water during dives) and 7% of daylight time in Alaska (Dzinbal and Jarvis 1984) and Iceland (Inglis et al. 1989), respectively. Excluding pause times during diving bouts, as in Dzinbal and Jarvis (1984), yields an estimate of 28% of daylight time spent feeding by prelaying females at Harlequin Brook. A high level of food availability was thought to account for low feeding rates in Iceland (Inglis et al. 1989). It also probably contributed to the lack of difference in the percentage of time spent feeding by males and females (Inglis et al. 1989), in contrast to the results of this study, the results obtained by Bengtson (1972) and Dzinbal and Jarvis (1984), and the differences typically observed in

Fig. 2. Diurnal feeding patterns of Harlequin Ducks in the prelaying to early laying, incubation, and brood-rearing periods on Harlequin Brook, Hebron Fiord, Labrador, in 1996.



other waterfowl (Krapu and Reinecke 1992). Higher feeding rates and greater differences between males and females in this study than in those of Bengtson (1972) and Dzinbal and Jarvis (1984) suggest that greater foraging effort was required from females at Harlequin Brook to meet the demands of egg production.

Changes in diurnal feeding patterns through the season may explain the differences in feeding patterns observed in previ-

Table 3. Comparison of dive and pause times and dive–pause ratios for paired males and females and unpaired females at Gooseneck Steadies on 19–21 June during the early laying period, females at Inukshuk on 15–18 July during the incubation period, and females at J-Kûk on 2–4 August during the brood-rearing period.

	Dive time (s)	Pause time (s)	Dive–pause ratio
Gooseneck Steadies			
Paired males	22.8±4.5 (278)	13.7±7.0 (228)	2.0±0.8 (228)
Paired females	21.5±5.9 (233)	11.9±5.8 (181)	2.2±1.0 (181)
Unpaired females	24.7±4.4 (85)	16.5±7.1 (73)	1.7±0.8 (73)
Inukshuk			
Females	10.0±4.3 (104)	7.6±5.3 (83)	2.2±1.9 (61)
J-Kûk			
Females	23.3±7.1 (178)	13.3±7.9 (155)	2.2±0.9 (155)

Note: Values are given as the mean ± SD. Numbers in parentheses are sample sizes.

Table 4. Presence (+) and percent composition of prey remains in Harlequin Duck feces collected on 3 July (30 individuals identified) and 4 August 1996 (4493 individuals identified) at Harlequin Brook, Labrador.

	3 July	4 August
Simuliidae (Diptera)	0	98.0
Trichoptera	+	0.7
Plecoptera	+	0.4
Ephemeroptera	+	0.1
Coleoptera	0	0.1
Hydracarina (Acari)	0	<0.1
Unknown	0	0.7

Note: Numbers of simuliid individuals were accurately determined by counting heads. Remains of other prey types were mostly leg parts, so numbers of individuals were more difficult to estimate.

ous studies. Observations revealed little variation during the prelaying period, as was found by Inglis et al. (1989) for the same period, and major peaks of activity in the morning and evening during incubation and brood rearing, similar to the overall summer patterns reported by Bengtson (1966, 1972) and Kuchel (1977). However, in contrast to Inglis et al. (1989), continuous feeding throughout daylight hours during the prelaying period could indicate low food availability at that time, resulting in the high proportion of time spent feeding by prelaying females. No evidence of nocturnal feeding was obtained, although sightings of flying and swimming birds at the estuary and J-Kûk indicated that some activity does occur in the predawn hours.

The extensive feeding in the slow-moving waters at Gooseneck Steadies was unexpected. Harlequin Ducks have rarely been sighted on lakes in Iceland (Bengtson 1966), and they mostly confine their feeding activity to swiftly running waters (Bengtson 1972; Kuchel 1977; Inglis et al. 1989). However, Kuchel (1977) reported frequent use of calm water and ponds during periods of high water and for brood rearing in Montana, and dense shrub cover was thought to attract Harlequin Ducks to a lake where a brood was successfully raised in Alaska (Dzinbal 1982). I suspect that Harlequin Ducks may have been nesting in the dense shrubs covering the islands in Gooseneck Steadies, where vegetation was similar to that of the islands where a nest was found above J-Kûk (Rodway et al. 1998). Trichoptera were abundant only at Gooseneck Steadies in June and may have been important in the diet at that time. In other habitats alternative foods may have been less available.

Fecal remains collected in August were composed primarily of simuliid larvae in a similar proportion to that reported in the diet for May to August in Iceland (Bengtson 1972). The fecal sample collected in early July differed most notably by the complete absence of simuliids. Simuliids also were not present in invertebrate samples taken in Harlequin Brook at the end of June, and were most abundant in August.

Diving was the predominant feeding behaviour for all classes of Harlequin Ducks, and for chicks formed a similar proportion of their feeding activity as skimming. In contrast, young chicks fed mostly by skimming in Iceland (Bengtson 1972) and rarely fed by diving until the age of 3–4 weeks in Montana (Kuchel 1977). Adult insects picked from the surface formed a large part of chicks' diet in Iceland (Bengtson 1972), and type of feeding behaviour probably relates to timing of insect emergence (Sedinger 1992). Much of the skimming behaviour recorded at Inukshuk was chicks scraping prey, possibly simuliid larvae or pupae, off shallow rocks. Adult black flies were also available at that time, as they emerged in large numbers for the first time in 1996 on 2–3 August (personal observation), coincident with the observations of brood-rearing behaviour. Greater handling time for adults (Sedinger 1992) may have made it advantageous for chicks to feed on the more concentrated larvae and pupae still attached to the substrate. At Gooseneck Steadies, chicks spent considerable time picking prey off the edge of the stream bank. Numerous Plecoptera were observed emerging along the stream edges at that time and may have been an important prey type. I have no information on the proportion of time spent feeding by harlequin chicks elsewhere, but the 45% I observed is similar to that reported for other diving species (Sedinger 1992).

The mean dive times of 22–24 s at Gooseneck Steadies and J-Kûk were longer than the means of 16 and 20 s reported by Bengtson (1972) and Kuchel (1977). Shorter dive times in the

shallower and faster water at Inukshuk were similar to those measured by Inglis et al. (1989). Maximum dive time was 35 s in this study and that of Bengtson (1972). Longer dives of 39 and 40 s duration have been recorded by Bengtson (1966) and Kuchel (1977), respectively.

Dive–pause ratios of 4.0 (Bengtson 1966; Kuchel 1977) indicated that Harlequin Ducks are the most efficient of sympatric diving ducks (Bengtson 1966, 1972). The lower ratios of 1.7–2.2 found in this study are similar to those reported for Oldsquaw (*Clangula hyemalis*), Red-breasted Merganser (*Mergus serrator*), and Barrow's Goldeneye (*Bucephala islandica*) in stream habitats in Iceland (Bengtson 1966). The similar dive–pause ratios at Gooseneck Steadies, Inukshuk, and J-Kûk imply that differences are not a function of habitat, water depth, or flow rate. There are no obvious methodological differences among studies, and reasons for the large discrepancy between my results and those of Bengtson (1966) and Kuchel (1977) are not apparent.

Low feeding rates for parents with broods and higher rates for birds without broods have been reported for other species (Afton and Paulus 1992). Kuchel (1977) reported that females rarely fed until their broods were several weeks old, but this seems unlikely, given the energy requirements of laying and incubation (Alisauskas and Ankney 1992). Alert behaviour by parent females was most common at Inukshuk and not recorded at Gooseneck Steadies, probably because of differences in habitat and feeding behaviour. At Inukshuk, where most feeding occurred towards the exposed center of the brook, the female often stood in alert posture on an exposed rock while her chicks were foraging. Most feeding by chicks at Gooseneck Steadies occurred close to shore while the female maintained a guarding position, swimming so as to keep her chicks between her and the shelter of the shrub-covered stream bank.

Streams used by Harlequin Ducks for breeding in boreal, subarctic, and montane areas have relatively low mean benthic animal standing crops and low productivity (Ulfstrand 1968; Bengtson and Ulfstrand 1971; Bengtson 1972). Low breeding density and a high frequency of nonbreeding, especially when productivity is reduced (Bengtson and Ulfstrand 1971), indicate that Harlequin Ducks are poorly buffered against variation in food supplies. Although feeding rates of prelaying Harlequin Ducks at Harlequin Brook were not high compared with those of some other waterfowl (cf. Krapu and Reinecke 1992), they were higher than those reported in other Harlequin Duck studies, and similar to or higher than those observed in other river ducks (Eldridge 1986*a*, 1986*b*). This suggests that there may be greater energy constraints on foraging effort in river specialists than in dabbling ducks or other diving species. The higher prelaying feeding rate I observed in calm waters at Gooseneck Steadies than in faster waters in other studies provides some support for this idea.

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