

## Feeding Behavior of Harlequin Ducks (*Histrionicus histrionicus*) Breeding in Newfoundland and Labrador: A Test of the Food Limitation Hypothesis

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We compared foraging behavior and productivity of harlequin ducks (*Histrionicus histrionicus*) in Newfoundland in 1997 and 1998, and central Labrador in 1997 to 2002, and tested predictions that productivity of this species is limited by available food. Females without broods were observed early in the nesting cycle (>70% of the local population), and were ascertained to be failed nesters. These adult females without broods were indicative of what previous researchers had defined as “nonbreeders.” Productivity of harlequin ducks breeding in central Labrador ranged from 10.0% to 88.9% of females producing broods with 1.00 to 3.38 young per female present, annually. Females spent relatively low proportions of time feeding (mean  $\pm$  SD:  $0.385 \pm 0.014$  of ~17 h of daylight), and there was low variability across time and space. Therefore we inferred that foraging behavior was not tracking a variable food resource, and birds could have budgeted considerably more time to feeding if this had been necessary to meet their nutritional requirements. Physical evidence of nesting, including anatomical and radiotelemetry data, indicated that all adult female harlequin ducks in our study area attempted breeding each year. We found no support for the paradigm that females were constrained by lack of sufficient food on their breeding habitat and deferred breeding. We suggest that hypotheses such as food limiting breeding productivity can be tested using behavior that can be readily quantified, and with greater rigor than attempting to measure aquatic epibenthos in fast moving rivers.

Key words: Harlequin duck; *Histrionicus histrionicus*; Feeding behavior; Nonbreeding; Food limitation; Prey switching

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Animals breeding in temperate environments exploit food resources that may be seasonally abundant (e.g., Fretwell, 1972) yet food supply often limits reproductive success and survival of young and/or adults (T. Martin, 1987). Lack (1968) proposed the food limitation paradigm for the K-selected life history patterns of seabirds, and suggested that these limits arise from the sparseness, patchiness, and variability of food supply. Long-lived birds should ac-

cept few risks for the sake of a single breeding episode so that they may enhance future reproductive success (Ricklefs, 1983). Thus, low reproductive rates and long life spans of seabirds may reflect evolutionary influences of environment and demographic consequences of interaction with the environment (Ricklefs, 1990).

Annual breeding propensity is thought to vary considerably in sea ducks (Goudie et al., 1994) and

contribute to large fluctuations in annual productivity (Coulson, 1984; Goudie, Robertson, & Reed, 2000; Milne, 1974). Nonbreeding in harlequin ducks has been defined as cases in which sexually mature females migrate to and reside on natal rivers during the spring–summer period but do not breed (Bengtson & Ulfstrand, 1971). Food limitation has been a plausible hypothesis explaining variability in breeding propensity and productivity in harlequin ducks because productivity and populations were weakly correlated with the quantity of epibenthic larval insect food available on the breeding streams in Iceland (Bengtson, 1972, Gardarsson & Einarsson, 1994). This is in contrast to DuBowy's (1988) assertion that no study had demonstrated a clear case where waterfowl populations were food limited during the breeding season. Individuals of most species are hypothesized to have an optimum time budget for environmental conditions, and selection should favor individuals whose time budgets are most favorably adapted (Verner, 1965). Consequently, low levels of available food should limit the ability of individuals to budget sufficient time for feeding, and this can be detected by field observations. In contrast, attempts to quantify epibenthos in rivers and streams in relation to productivity are very difficult and results lack precision (Bengtson & Ulfstrand, 1971).

Direct behavioral and/or physiological evidence for facultative deferment or “skipping” of breeding in some years is scarce. A physiological mechanism for such a phenomenon is an important consideration, and decisions to breed must occur weeks before the laying period because biosynthesis and egg formation may often occur before females can assess or benefit from increased food availability near the breeding site (Williams, 1999). Based on this background, we tested the implications to foraging behavior imposed by limiting food availability using data on behavior of harlequin ducks breeding in Labrador and insular Newfoundland. Harlequin ducks acquire their nutrition for reproduction on the breeding grounds (Robertson & Goudie, 1999), and therefore we expected harlequin ducks to allocate a large and variable proportion of the day to feeding. We expected considerable variation across sites and years.

Specifically, our predictions were:

**Prediction 1:** If food was limiting breeding propensity by females, we expected that harlequin ducks

would budget a high proportion of the day to feeding. In other words, a large proportion of the day would be budgeted to feeding activity in order to meet metabolic requirements for egg production.

**Prediction 2:** Because productivity varies across sites, we expected to observe high variance in feeding behavior among sites in Labrador and Newfoundland if this variability was attributable to food availability.

**Prediction 3:** If adult females “defer” or skip breeding, we expected pairs to remain intact on the breeding streams until such time as males depart for their marine molting sites. In other words, we did not expect to observe males unaccompanied by their mates, and/or paired females alone during the spring observation period if females were not breeding.

**Prediction 4:** If females skip breeding we do not expect to see evidence of egg passage in the form of physiological and physical changes of anatomy.

## Methods

### *Behavior*

During the spring–summer period from 1999 to 2002, we searched for apparently nonbreeding adult female harlequin ducks (criteria based on Bengtson & Ulfstrand, 1971) on our study areas at Fig River (53° 03' N, 63° 09' W), and at Crooked River (54° 06' N, 60° 48' W) near Nipisish Lake in central Labrador. Relatively large concentrations of breeding harlequin ducks were known for these watersheds that typically displayed considerable rapids and riffles with numerous small ponds. Although harlequin ducks utilized 10–15 km of these reaches, they especially concentrated at the outlets of Fig Lake and Nipisish Lake (Goudie, 2004). We compared our findings in Labrador to results obtained by the senior author on the Torrent River in northern Newfoundland (Goudie & Gilliland, 2005).

Behavior of harlequin ducks was quantified in spring (May 10–June 18) using an instantaneous focal sampling approach (Altmann, 1974) linked to marked individuals. This was possible because harlequin ducks are philopatric to breeding sites (Robertson & Goudie, 1999), and a large proportion of individuals on the study area were marked using field-readable colored alphanumeric tarsal bands. The issue of pseudoreplication was debat-

able because behavior was the unit of sampling and individual birds were resampled in different habitats and locations. Nevertheless, we controlled for variance attributable to individuals in a General Linear Model, and present both approaches.

Behavior of harlequin ducks was characterized by bouts or states (e.g., feeding and resting; see P. Martin & Bateson, 1986), and each of these bouts generally lasted less than 30 min. Focal birds were monitored for 30 min (or until lost from sight) using binoculars and/or (20–60×) spotting scopes. Instantaneous behavioral classifications of focal birds were recorded every 15 s (every 60 s in 1999) using digital watches with countdown-return beeper functions) from a suite of 60 categories until 30 min had elapsed. We attempted to sample equally throughout the daylight period. In our analysis, we focused on the proportion of time spent feeding by paired female harlequin ducks. In order to maximize independence of behavioral data, a new bird was selected for observation or observers shifted locations to find other birds after each 30-min watch was completed. In a few cases, two standardized watches were conducted in succession.

Instantaneous data recorded every 15 s were not statistically independent within each 30-min watch. Therefore, frequencies within behavioral categories were summed over each watch, and these summaries were converted to proportions that represented the primary unit for further analyses (i.e., one data entry per behavioral watch of 30 min) (Goudie & Ankney, 1986; P. Martin & Bateson, 1986).

#### *Morphometrics and Evidence of Breeding*

Adult harlequin ducks were captured by suspending 18 × 3-m mist nets across rivers, usually in early morning (0500–0800 h) when birds flew frequently. During high water, we erected mist nets in L-shaped patterns at the mouths of coves frequented by harlequin ducks. The birds were flushed into nets by concealed observers as birds fed along the inundated shorelines of these coves. After removal from mist nets, the harlequin ducks were placed in mesh bags, and shielded from visual stimuli by covering bags with a dark cloth. Birds were banded on the right tarsi using standard USFWS stainless steel bands, and marked on the left tarsi with a yellow plastic band bearing a two-digit numeric-alpha code that could be deciphered through 15–60× spotting

scopes when birds were roosting on rocks and ledges.

Bengtson and Ulfstrand (1971) inferred that all females without broods that were captured on their study area(s) in Iceland were adults. They did not define any criteria for separating adult females from subadults or juveniles. We assumed that the absence of a full or reduced bursa of Fabricus qualified individual females as adults (see Mather & Esler, 1999). On our study area, individual birds were measured, and members of pairs were released together.

Morphometrics were collected on captured birds, including mass and length of wing chord, ninth primary, tarsus, tail, culmen midline, and sternum. The following criteria (after Allen, 1985) were indicative of recent egg laying: (i) splayed pelvic bones that easily allowed the passage of two fingers (~4 cm) when moved over the lower abdomen, (ii) the obvious presence of an egg in the oviduct (i.e., a hard bulge protruding in the lower abdomen), (iii) a sunken lower abdomen indicating that an egg had recently been laid. As the egg matures in the abdomen and the shell is secreted, the egg can be detected as a hard bulge in the normally soft area of the abdomen. With egg passage, the pelvic bones that are normally “closed” across the abdomen to within about 1 cm of each other become splayed more than 2 cm, and the abdomen displays a “sunken” appearance.

#### *Productivity and Breeding Propensity*

Productivity, indexed as broods and young per adult female present on the study area, was quantified annually from frequent searches of the study areas for broods, and linked to marked (or unmarked) females whenever possible. All broods were assumed detected because we frequently surveyed our study areas throughout the breeding seasons. Nevertheless, this measure underestimated nesting effort because females that failed during laying and incubation remained unknown. Therefore, to detect early nesting failure at Fig River, subsamples of females were captured prior to the laying period and fitted with radio transmitters in 2000 ( $n = 4$ ) and 2001 ( $n = 5$ ) attached by anchor sutures to the interscapular area of paired females (Pietz, Brandt, Krapu, & Buhl, 1995). We searched for radioed females during daily routine collection of behavioral data that was concentrated in a 1-month period from mid-May to mid-

**Table 1.** Numbers of Female Harlequin Ducks and Productivity at Fig River, Labrador in 1999–2002.

|   | 1999            | 2000            | 2001            | 2002            |
|---|-----------------|-----------------|-----------------|-----------------|
| Total females present                               | 15 (12)         | 12 (11)         | 17 (10)         | 13 (12)         |
| Lone females  | 10 (8)          | 9 (8)           | 11 (8)          | 9 (9)           |
| Females with broods                                 | 5 (4)           | 3 (3)           | 6 (2)           | 3 (3)           |
| No. of young  | 25 (18)         | 17 (17)         | 29 (9)          | 13 (13)         |
| Brood size (mean $\pm$ SE)                          | 4.40 $\pm$ 0.68 | 4.67 $\pm$ 0.68 | 4.83 $\pm$ 0.54 | 4.67 $\pm$ 0.88 |
| Marked females with broods (proportion with broods) | 4 (0.33)        | 3 (0.27)        | 2 (0.20)        | 3 (0.25)        |
| Young per female with broods                        | 5 (4.5)         | 5.6 (5.6)       | 4.8 (4.5)       | 4.3 (4.3)       |
| Young per female present                            | 1.67 (1.50)     | 1.42 (1.55)     | 1.71 (0.90)     | 1.00 (1.08)     |

Note: Unless otherwise specified, numbers in parentheses indicate number of marked birds.

June. Daily coverage of rivers varied from 1 to 6 km of the study areas. Some radio signals went out of range, and we subsequently deployed helicopter searches to locate these individuals. We followed up on radioed individuals detected from helicopter by visiting the reach of river by foot over the following days. We located nest sites by triangulating approximate positions of incubating females, and then homing into exact locations when possible (in one case the river could not be crossed due to high water). In all cases, females flushed from the nest when approached within 2 m. Radiotelemetry also helped us to assess the accuracy of the morphological indicators of egg passage noted above.

## Results

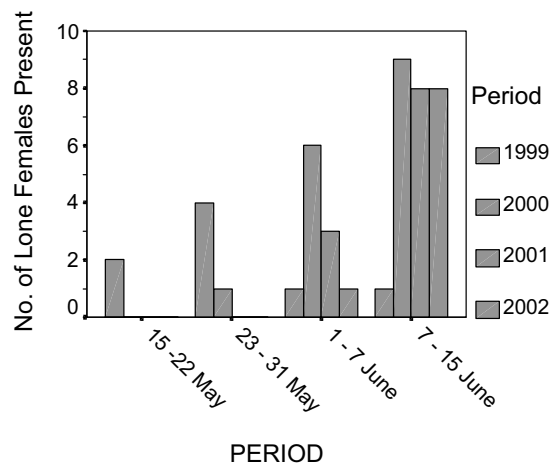
### *Presence of Females Without Broods, Productivity, and Pair Bonds*

At Fig River, by early to mid-June of each year (by which time all females seen later with broods had to have laid eggs), there were noticeable numbers of marked adult females present without males or broods (mean  $\pm$  SD: 8.25  $\pm$  2.71, range 9–11, Table 1). We noted that the relatively early breeding chronology observed in 1999 resulted in the presence of “lone females” as early as May 15–22. In 2001 and 2002, “lone females” were not detected until early June (Fig. 1). These represented “nonbreeding” harlequin ducks as defined by Bengtson and Ulfstrand (1971).

The proportion of female harlequin ducks with broods was not detectably different among years at Fig River in central Labrador (range 20% to 0.33% of marked females,  $\chi^2 = 0.37$ ,  $p = 0.95$ ) (Table 1)

but was significantly lower than that of Torrent River in northern Newfoundland in 1997 (75%,  $\chi^2 = 6.28$ ,  $p = 0.01$ ), and in 1998 (88.9%,  $\chi^2 = 11.36$ ,  $p = 0.0008$ ) (Goudie & Gilliland, 2005) but similar to Crooked River, Labrador (in 2000, 10%,  $\chi^2 = 1.84$ ,  $p = 0.17$ ; in 2001, 17.6%,  $\chi^2 = 0.81$ ,  $p = 0.37$ ). At Fig Lake, young per female present was lower in 2002 than in previous years ( $\chi^2 = 7.31$ ,  $p = 0.009$ ) (Table 1), and much lower in all years than at Torrent River in northern Newfoundland (2.50 and 3.38 young per female present;  $\chi^2 = 25.32$ ,  $p < 0.001$ ).

Our data did not support the prediction that females had “skipped” breeding because, overall across years, about 25% of pair bonds had dissolved by May 31, a further 33% by June &, and most pair bonds were dissolved by June 15 in most years (Table



**Figure 1.** Number of lone female harlequin ducks observed at Fig River, Labrador, by observation period and year. Surveys period was early May to late June in all years.

**Table 2.** Proportion of Pair Bonds Intact by Time Period for Fig River, Labrador, 1999–2002

| Period        | 1999 ( <i>n</i> = 8) | 2000 ( <i>n</i> = 12) | 2001 ( <i>n</i> = 11) | 2002 ( <i>n</i> = 12) |
|---------------|----------------------|-----------------------|-----------------------|-----------------------|
| Before June 1 | 0.375                | 0.33                  | 0.272                 | 0.083                 |
| June 1–7      | 0.125                | 0.25                  | 0.364                 | 0.083                 |
| June 8–15     | 0.375                | 0.25                  | 0.364                 | 0.334                 |
| After June 15 | 0.125                | 0.17                  |                       | 0.500                 |

2). Breeding chronology was relatively late in 2002. By the early to mid-spring period there were adult female harlequin ducks present on our study area without mates. These adult females had previously been paired and qualified as nonbreeders as defined by Bengtson and Ulfstrand (1971).

#### *Time Budgeted to Feeding*

Our data did not support the prediction that foraging rates would increase in years or sites of low annual productivity because there was no correlation between annual productivity and proportion of time spent feeding ( $p = 0.932$ ). Paired female harlequin ducks at Fig River budgeted an average of 38.4% of the 17 h of daylight to feeding (Fig. 2), and we did not detect a diurnal pattern. Feeding rates by paired female harlequin ducks were similar across years [ $F(3, 826) = 1.36, p > 0.50$ ] and the statistical support was less compelling across sites in our study [central Labrador,  $F(4, 1028) = 2.205, p = 0.067$ ]. We controlled for variance associated with the sampling of known individuals at Fig River, and this is also corroborated that there were no significant differences in feeding rates across years [ANOVA block design:  $F(3, 31) = 1.062, p = 0.433$ ].

The lack of variation in feeding rates across sites did not support our prediction that food may be limiting productivity because proportion of time spent feeding in central Labrador was strikingly similar to time/activity budgets calculated elsewhere in Newfoundland and Labrador [i.e.,  $0.39 \pm 0.051$  (SE) for northern Newfoundland in Goudie & Gilliland, 2005; 0.396 for northern Labrador in Rodway, 1998] (Fig. 3).

#### *Morphological Evidence of Breeding*

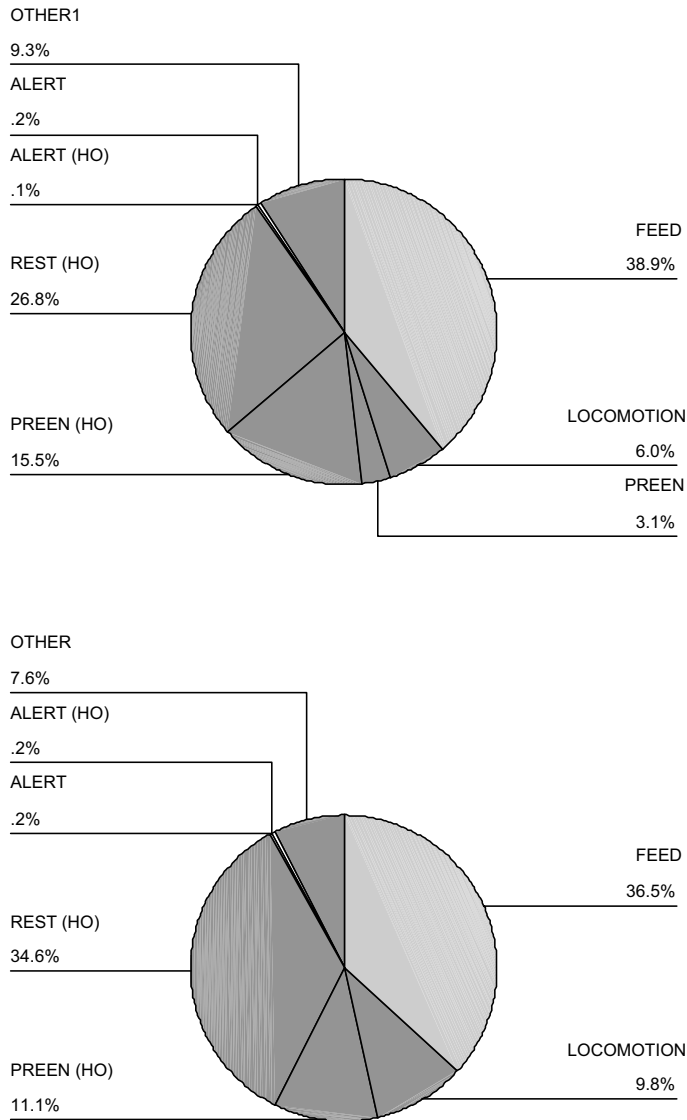
In the study areas in central Labrador, six female harlequin ducks known to be laying and/or incubating eggs corroborated the criteria defined as evidence

of egg passage (i.e., splayed pelvic bones, sunken abdomen, and/or mature egg present in oviduct). Based on radiotelemetry we were able to confirm their nesting status.

In 1999, 2000, and 2001, 27 females were captured in the spring–early summer period (May 15–June 7). Our data did not support the prediction that apparent “nonbreeders” would show no evidence of egg passage because external examination of the lower abdomen of these individuals indicated that 23 had laid eggs. Based on presence of a reduced bursa of Fabricius, females identified as subadults ( $n = 2$  at Fig River,  $n = 1$  at Crooked River) did not show evidence of egg formation or passage (Table 3).

#### *Evidence From Radiotelemetry*

Intact pair bonds were last observed for female harlequin ducks on June 7, 2000, and May 24, June 5, and June 15, 2001. In 2000, we located one successful nest 500 m below the outlet of Fig Lake, and we hypothesized that nests may be depredated early in the nesting cycle because three of the four radioed females outfitted with radiotransmitters disappeared from this general area (out of range), and reappeared 2–3 weeks later. They remained there without broods until departure later in the summer. One female had sustained a wound on the neck consistent with an encounter with a predator. Therefore, in 2001 we tracked five females at Fig River soon after they were released with attached radiotransmitters. Of these five females, three nests were located, of which two failed due to egg depredation. Of the two remaining females, one was believed to have failed because it was previously triangulated across the river at a potential nest site, and the other was 2 years old and appeared not to have nested. The failed females, excluding the 2 year old, were subsequently regularly observed on the study



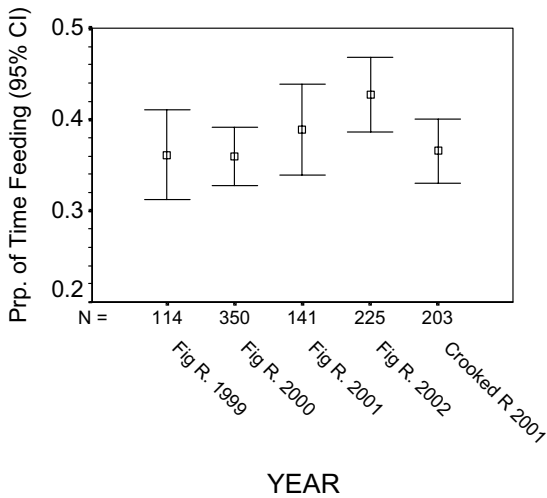
**Figure 2.** Behavior of adult female harlequin ducks at Fig River (top,  $n = 141$ ) and Crooked River (bottom,  $n = 203$ ), central Labrador, 2001. (HO) represents out of water.

area up to early July. None of the females that failed their initial nesting attempted to renest. This included a female in 2001 that lost her initial clutch before it was completed.

### Discussion

We believe more empirical research is required to definitively test the deferred breeding hypoth-

esis. There were relatively low proportions of the daytime budgeted to feeding by paired female harlequin ducks (i.e., 35–40% in our study), which is similar to other areas of the species' range (see Robertson & Goudie, 1999). We infer that this is not consistent with the food-limiting hypothesis proposed by Bengtson (1972) and others (Gardarsson & Einarsson, 1994; Rodway, 1998) because it would predict that proportions of time



**Figure 3.** Proportion of time budgeted to feeding by adult female harlequin ducks in spring at Fig River and Crooked River, Labrador, 1999 to 2002.

budgeted to feeding by adult female harlequin ducks should be variable, reflecting differences in food abundance among sites and across years. Bengtson (1972) proposed a food limitation hypothesis based on the coincidence of low productivity (described as frequency of nonbreeding) with relatively low total standing crops of dipteran larvae in 1970 compared to 1969 (Bengtson & Ulfstrand, 1971). However, closer inspection of those data indicated wide interyear variance that was not significantly different across years.

We suggest that individual harlequin ducks could have budgeted more time to feeding had it been necessary (e.g., Goudie & Ankney, 1986; Goudie & Hearne, 1997). Some species of birds are capable of increasing their ingestion rate under different regimes of food availability (Swennen, Leopold, & de Bruijn, 1989). Our results underline the importance of testing prevailing paradigms with behavioral information, because high proportions of time spent foraging are expected if food is scarce and hence would limit productivity of females. Furthermore, quantification of epibenthic insect larvae in fast moving rivers and streams is onerous, lacks a rigorous methodological protocol, yields data with extremely high variance, and ultimately interferes with the foraging activities of the study birds.

Many studies of harlequin ducks reported observations of adult females without broods present well into the brood season (Robertson & Goudie, 1999). We believe that the evidence for the existence of “nonbreeding” females is suspect because adult females without broods present on our study area had failed at nesting. Because nest failure often occurred relatively early in the nesting cycle, pair bonds were sometimes still intact or lone females were subsequently present without broods. There was no evidence of reneesting despite, in some cases, the pair bonds still being intact when the original (partial) clutch was depredated. Bengtson (1972) concluded that nest failure had little or no influence because 77 of 89 (87%) of monitored nests in Iceland were successful over 4 years of study. Hence he concluded

**Table 3.** Physical Examination of Captured Female Harlequin Ducks for Evidence of Breeding at Fig River, Labrador, 1999–2001

| Area/Date              | No. Examined (With Broods) | Open Pelvis & Dilated Cloacum | Sunken Abdomen | Egg in Oviduct     | No Evidence of Breeding |
|------------------------|----------------------------|-------------------------------|----------------|--------------------|-------------------------|
| Fig River              |                            |                               |                |                    |                         |
| May 18–June 9, 1999    | 9 (3)                      | 7                             | 1              | 1 (1) <sup>a</sup> |                         |
| June 3–7, 2000         | 4 (1)                      | 2                             | 1 <sup>b</sup> | 1                  |                         |
| May 20–25, 2001        | 5 (1)                      | 2                             |                | 2                  | 1 subadult              |
| June 7, 2002           | 3                          | 2                             | 1              |                    |                         |
| Crooked River          |                            |                               |                |                    |                         |
| May 17–18, 2001        | 2                          | 1                             |                |                    | 1 subadult              |
| May 30–June 1, 2001    | 4                          |                               | 1              | 1                  | 2 <sup>c</sup>          |
| Total Spring 1999–2002 | 27 (5)                     | 14                            | 4              | 5                  | 2 subadult, 2 adult     |

<sup>a</sup>Recapture of previously examined individual.

<sup>b</sup>Nest found.

<sup>c</sup>2-year-old females with no evidence of breeding.

that the presence of adult females without broods on the breeding streams must have, in part, represented birds that deferred breeding for that year. Because nests in his study were found by manual searching, his observations were limited to specific locations such as midstream islands, and those samples may not have been representative.

In wild birds, it is widely assumed that reproduction is both energetically and nutritionally expensive. There is often marked interindividual variability in reproductive traits, and a few individuals repeatedly contribute most of the offspring to the population (Newton, 1986; Williams, 1999). Consistent with a behavioral/physiological-based system, Coulson (1984) speculated that common eiders (*Somateria mollissima*) reduce the risk of death caused by the stress of breeding by avoiding nesting in certain years. However, direct evidence for deferred breeding or nonbreeding in the context of a decision-based system on the breeding ground is still lacking because Coulson (1984) based his inference on an "uncatchable" portion of the population that was not banded. This "uncatchable" component was assessed for band status when females flushed from nest sites on the colony. Our experience, and that of others (S. Jamieson, personal communication), is that this technique is biased against detecting banded individuals because the tarsus is rapidly drawn under the flank feathers when birds flush. Without the unbanded component of "uncatchable" birds, the results presented by Coulson (1984) might not support the paradigm of deferred, or lack of, breeding in common eiders or speculated for other species of sea ducks (Bertram, Lack, & Roberts, 1934; Bird & Bird, 1940).

Cyclic predator-prey models have been described for many species in the north boreal zone (Boutin et al., 1995; Krebs, Boutin, & Boonstra, 2001). Increased productivity as a result of release from predation pressure during years of rodent abundance has been demonstrated for long-tailed ducks (*Clangula hyemalis*) (Pehrsson & Nystrom, 1988) and could be important for harlequin ducks breeding in central Labrador because there were fewer young per female in 2002 when rodent populations were very low (personal observation). Some authors have noted a link between breeding propensity of Arctic-nesting bird species and lemming abundance (e.g., Blomqvist, Holmgren, Åkesson, Hedenström, & Petterson, 2002; Quakenbush & Suydam, 1999;

Summers & Underhill, 1987; Underhill et al., 1993), supporting a predator-based model of prey switching.

Perhaps the situation in Labrador is unique, but the proportion of time spent feeding by females in Iceland (~7% in Inglis, Lazarus, & Torrance, 1989) is not consistent with the food-limiting hypothesis. Their methods may have underestimated the actual time spent feeding because individuals that were under water were likely missed during scan sampling. Gardarsson and Einarsson (1994) presented 14 years of data on insects (Diptera) and productivity of harlequin ducks on river Laxá at Lake Myvatn that clearly appear cyclic, which is consistent with the reciprocal model of predator-prey. Productivity in western North America also varies substantially (Robertson & Goudie, 1999), and recent radiotelemetry work by Smith (2000) in Alberta confirmed that 15 of 17 tracked female harlequin ducks attempted nesting, and the remaining two may have failed nesting.

An alternative to the food limitation hypothesis emphasizes an environmentally imposed cyclic variation in depredation to account for variation in annual productivity of harlequin ducks. Nevertheless, we do not rule out that this sea duck may defer breeding in some years by remaining in coastal habitats or that our results are unique to Labrador.

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