FEEDING SCHEDULE AND DAILY FOOD CONSUMPTION IN RED-THROATED LOONS (*GAVIA STELLATA*) OVER THE PREFLEDGING PERIOD

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ABSTRACT.—We describe parental feeding activities of Red-throated Loons (*Gavia stellata*) throughout the prefledging period at two freshwater nesting territories in coastal British Columbia. The nesting lake contained resident fish populations, but adult loons fed marine fish to their young, making an average of 11 flights per day (average duration 60 min per flight) to the ocean and returning each time with a single fish. Small shallow-bodied fish (Ammodytidae, Pholidae), which were easily swallowed by chicks, predominated in the diet during the 3 days following hatching. The total weight of fish fed to the chicks per day (8–194 g) increased over the prefledging period: adults returned fewer but larger fish (Embiotocidae) as the chick aged. Of the fish offered, 4% were too large for the chick to swallow.
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UNLIKE other Gaviidae, which forage for their young in or near their freshwater nesting territory, Red-throated Loons (*Gavia stellata*) often nest on small tarns and fly to larger lakes or the ocean to obtain food for the young (Palmer 1962, Davis 1972, Bundy 1976). The diet of Red-throated Loon chicks has not been examined systematically, but it is known that small fish, swallowed whole, are the major food (Johnson and Johnson 1935, Davis 1972, Norberg and Norberg 1976).

Flights between the nesting territory and distant fishing areas involve a major energy expenditure (Norberg and Norberg 1976, Norberg 1981), and nesting success is inversely related to the distance that adult Red-throated Loons must fly to obtain food for the young (Davis 1972). Body weight increases from about 60 g at hatching to 1,600 g at fledging (Davis 1972), and parental feeding probably occurs throughout the 7-week prefledging period (Sjolander pers. comm.). One would expect a species under these constraints to exhibit foraging adaptations that minimize flight while maximizing caloric benefit to the young (Krebs 1978), such as returning with very large fish or using prey items when available from the nesting lake. Prey size, however, will be limited by flight aerodynamics (Norberg and Norberg 1976) and by the swallowing capabilities of the young (Pearse 1946, Rankin 1947, Davis 1972). To determine the response of adult loons to the increasing food demands of the young, we examined parental feeding behavior at two nest sites throughout the prefledging period.

STUDY AREA AND METHODS

We conducted observations at the Drizzle Lake Ecological Reserve (53°56'N, 132°05'W), Queen Charlotte Islands, British Columbia. Two nests (1979, 1982) were located on the 112-ha lake and one nest (1981) was on a 1-ha tarn in a large area of *Sphagnum* bog 1 km south of the lake. Drizzle Lake has resident populations of salmonids (*Salmo clarki, Salvelinus malma, Oncorhynchus kisutch*) and threespine stickleback (*Gasterosteus aculeatus*), as well as littoral macroinvertebrates such as trichopteran and odonate larvae; fish are absent in the tarn. Further descriptions of the habitat and its avifauna are given in Reimchen and Douglas (1980, in press).

We recorded all activities associated with the feeding of the young at the three sites from blinds within 8 m of the nest, with total observation periods of 285 h (1979), 22.7 h (1981), and 338 h (1982). In 1982, we made observations continuously from predawn through to darkness for a total of 21 days, including the first 6 days following hatching. Thereafter, we made observations at intervals distributed over the remaining prefledging period. When fledged, the young abandoned the lake with the adults, moving

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to coastal marine waters. At the 1979 nest, one chick was found dead on the morning of Day 2; the second fledged at Day 51. In 1981, both chicks were taken by a Bald Eagle (*Haliaeetus leucocephalus*) at an estimated age of 8 days. At the 1982 nest, one of two chicks fledged (Day 49); the second was captured by a Bald Eagle on Day 13. The 1982 nest was located on a floating platform (1 m^2) anchored 2 m from shore; we constructed this platform because, in previous years, rapidly changing water levels in early summer had flooded the shoreline nest at this site.

Small fish (which were always held crosswise in the adult's bill) were the only prey item offered to the young; these were identified by means of spotting scopes (20–50×), supplemented by 35-mm slides. In 1981 and 1982, 164 of the 264 observed feedings were recorded on a Sony portable VTR (Zoom and 1,000-mm lenses), and the tapes were later analyzed to determine taxa and size of prey, manipulation time, and details of feeding behavior. The length and depth of fish, in relation to the distance between the tip of the bill and the anterior edge of the eye of the adult loon, were measured on stop-action frames of the video tapes in 54 feedings (those in which the bill and prey were perpendicular to the axis of the TV lens). Where possible, we made measurements from two or three different frames of the same feeding. Body depth was converted to total length by means of standard ratios (Hart 1973). Mean fish length was calculated from all values and converted to actual length by means of reference measurements of the distance between bill tip and anterior edge of the eye (male, $\bar{x} = 81.0$ mm, $n = 4$; female, $\bar{x} = 73.1$, $n = 8$) on 12 Red-throated Loon skins.

For each species of fish, museum specimens (n = 6–12) with length and depth ranges similar to those observed during feedings were weighed (wet weight). Although the use of preserved specimens could underestimate live weight by 5–10% (Le Brasseur pers. comm.), we used unadjusted weights. We then established a length/weight curve, estimated the weight of each fish fed to the chick from the curve, and calculated the daily food intake for the prefledging period. For feedings from which no fish measurements were obtained but prey identification was possible, the mean weight of the appropriate group was used.

RESULTS

General feeding activity.—Feeding sequences were broadly similar throughout the prefledging period at the three nest sites: one of the adults flew to a marine inlet 3 km to the west and, after approximately 60 min (range 11–516 min, $n = 347$), returned with a single marine fish (occasionally still alive). Chicks took the prey directly from the bill and always swallowed the fish whole and head-first. During manipulation, the young often dropped the fish, more frequently in the first 5 days than from Day 6 to fledging (66.7% of the feedings vs. 21.8%, 1982 data); one or both of the parents dove and returned the dropped fish, offering it again. Immediately after the chick swallowed the fish, the adults dove in a response similar to that occurring when the fish had been dropped. When a chick failed to eat (see below), the adult that had made the feeding flight ate the fish.

Feeding schedule.—Foraging flights occurred throughout the daylight period but extended into twilight during the first 2 weeks following hatch. There was a marginal but nonsignificant increase in the number of flights near dawn and dusk (Chi-square = 3.40, df = 3, $P > 0.3$). The adults brought approximately 11 fish per day to the chicks over the prefledging period (1979, $\bar{x} = 11.2$; 1982, $x = 11.0$), although daily numbers were greatest during the first 12 days (Fig. 1). During this period, two chicks were present at the 1982 nest and one at the 1979 nest, yet the numbers of fish brought daily were only slightly higher in 1982 ($\bar{x} = 14.2$ and $\bar{x} = 12.4$, respectively; $t = 1.54$, $P > 0.1$).

Some of the fish were not eaten by the young (1979, 12.7%; 1982, 18.7%), but the numbers of feeding failures decreased rapidly as the chicks aged (Fig. 2). In 10 instances of the 45 failures of the young to eat fish (1982 data), a disturbance [e.g. presence of Common Loons (*Gavia immer*) in the territory, a Bald Eagle in flight] caused the adult to swallow the fish, usually before offering it to a chick. In 14 instances chicks were "not hungry" (i.e. did not approach the adult), in 15 the fish offered was too large for the chick to swallow, and in 6 cases the reason for failure could not be categorized. When the fish was too large or the chicks did not appear to be hungry, the adult continued to hold or offer the fish (range 5–18 min) before swallowing the fish itself.

Prey species.—Although freshwater fish were common in two of the nesting territories, 401 of the 402 observed feedings involved marine fish representing at least six families. The most common groups (1982) were Clupeidae/Osmeridae (herring/smelt) and Embiotocidae (seaperch), followed by Ammodytidae (sandlance) and Gadidae (cod) (Table 1). In 1979, approximately 20% were sandlance, and the remaining, which could not be positively identified, were probably herring and smelts; in 1982, 15 of the 19 fish brought to the chick

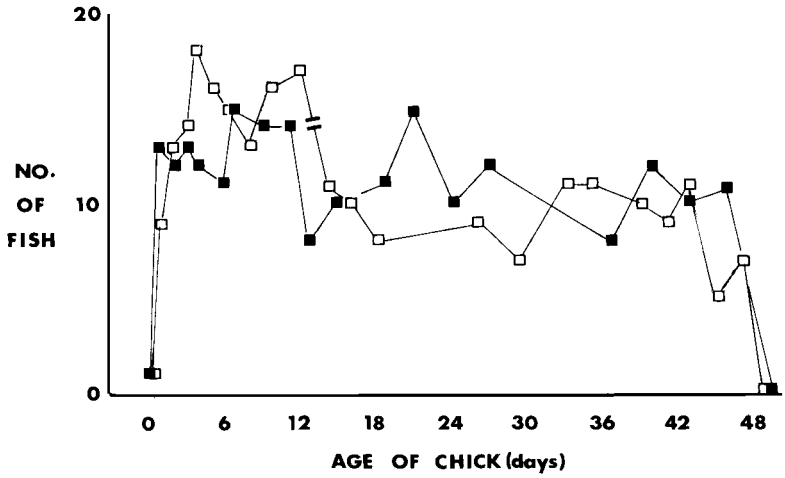

Fig. 1. Relationship between number of marine fish brought by adults and age of young. Solid symbol: 1979 nest (1 chick); open symbol: 1982 nest (2 chicks). Break at Day 13 in 1982 indicates death of one chick. The young left the lake when fledged.

were sandlance and 4 were seaperch. Only one freshwater fish was offered to the chick, a threespine stickleback captured from the nesting lake in 1979.

Marine fish were of three general size and weight classes: (1) small and shallow-bodied (sandlance and gunnel), (2) intermediate (herring, smelt, cod, prickleback, and unidentified), and (3) large and deep-bodied (seaperch). The proportions of each group in the diet varied with the age of the chick (Fig. 3). During the first 2 days after hatch, sandlance and gunnel predominated; these rapidly decreased in importance as the frequency of intermediate-sized fish increased. In the 2 weeks before fledging, intermediate-sized fish declined, and the diet of the chick was primarily seaperch.

The ability of the chicks to manipulate and swallow these different-sized classes of prey is also age-related (Fig. 4). During the first 7 days after hatch, 6.9% of sandlance and gunnel, 34% of intermediate-sized fish, and 100% of seaperch were not eaten. Failure to swallow large fish was a result of excessive depth rather than length of the fish. By the third week, the chick was capable of swallowing all fish offered.

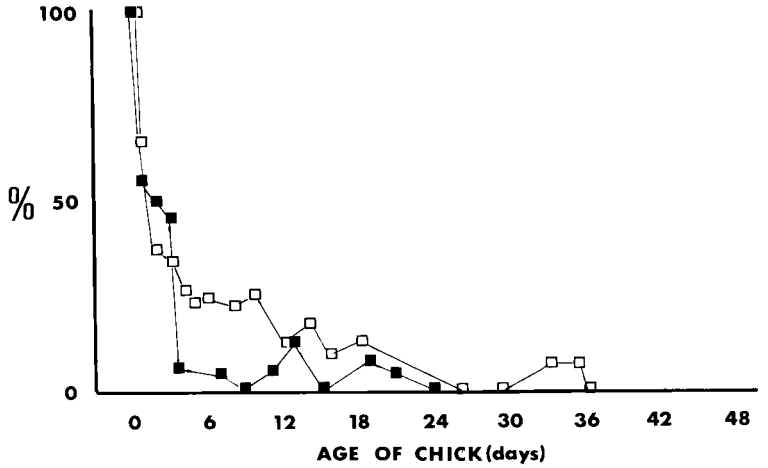

Fig. 2. Percentage of feeding failures in relation to age of young. Solid symbol: 1979; open symbol: 1982.

TABLE 1. Size estimates and numbers of marine fish brought by adult Red-throated Loons to flightless young [n = number of fish measured from videotapes and photographs; length : depth ratio from Hart (1973)]. Unidentified fish (N = 22) were approximately of a size and depth similar to Gadidae and were assigned a weight of 8.0 g.

Taxa	Total brought	n	Length (mm) $\bar{x}$ (range)	Length : depth	Weight (g) $\bar{x}$ (range)
Ammodytes hexapterus (sandlance)	29	9	79.2 (50–96)	9:1	1.5 (0.6–3)
Pholis sp. (gunnel)	5	4	85.3 (83–87)	9:1	4.1 (2–6)
Lumpenus sagitta (snake prickleback)	8	2	137.0 (127–147)	12:1	7.0 (6–8)
Gadidae (cod)	28	11	90.2 (75–105)	5:1	8.0 (4–13)
Clupeidae, Osmeridae (herring, smelt)	73	15	107.4 (65–137)	4.5:1	10.5 (4–24)
Cymatogaster aggregata (shiner perch)	66	19	106.4 (63–143)	2.5:1	22.5 (8–57)

During intervals between parental feedings, the chicks made short diving bouts in shallow water (< 1 m) and regularly surfaced with mosses, algae, or sedges in the bill. During the 2 weeks before fledging, the chicks raised on the lake dove in deeper water (1–3 m), yet in only 1 of over 200 dives observed was a fish (a threespine stickleback, estimated length 70 mm) returned to the surface. Marine fish brought by the parents during this period were immediately eaten by the young, and, because persistent begging was common, we assume that few freshwater fish were captured and consumed underwater.

Daily food intake.—Daily consumption of fish increased with the age of the young, ranging from 8.2 g on the day following hatch to 194 g before fledging. This represents a mean of 15.7% (range 7.3–24.5%) of the body weight per day (daily weights for *G. stellata* extracted from growth curve in Davis 1972). We calculated the predicted daily food consumption by deriving values for existence-energy requirements at 15°C (Kendeigh 1970) and by assuming a digestive efficiency of 70% (Wiens and Scott 1975) and a caloric equivalent of 1.5 kcal/g for fish (Cummins and Wuycheck 1971). It is evident (Fig. 5) that actual daily food consumption was lower than predicted values over much of the prefledging period, although the total weight of food brought by the adults was similar to predicted values during the first 18 days following hatch.

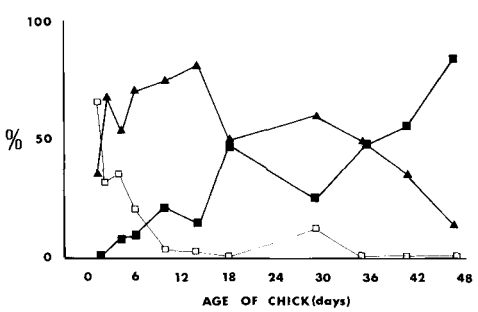

Fig. 3. Percentage of each prey group in relation to age of young (1982 data only). Open square: small and shallow-bodied fish (sandlance, gunnel); triangle: intermediate-sized fish (herring, smelt, cod, prickle-back, unidentified); solid square: large, deep-bodied fish (shiner perch).

DISCUSSION

The diet of Red-throated Loon chicks described in this study is comparable to that described by Johnson and Johnson (1935) in eastern Canada (sandlance, gunnel, and capelin), by Davis (1972) in the Canadian Arctic (capelin, slender eelblenny, sandlance, arctic char, grayling, and sculpin), and by Furness (1983) on the Shetland Islands (sandlance and gunnel). Feeding rates also appear to be similar. Davis (1972) recorded 94 feedings in 154 h of total observation time, a rate of 0.61 fish/h. Our data yield rates of 0.54 fish/h in 1979 and 0.71 fish/h in 1982. Weight and size of prey have not been previously described in detail, although in Sweden, 11 fish fed to nearly fledged chicks averaged 55 g and 15.6 cm (Norberg and Norberg 1976). These values are marginally higher than our estimates for seaperch fed to the young just before fledging.

The total weight of fish brought by the adult loons increased throughout the prefledging period. This was the result of increased size of fish rather than increased numbers of foraging flights. Adult loons gradually shifted from bringing predominantly small- and intermediate-sized species (such as sandlance and herring) shortly after chicks hatched to bringing

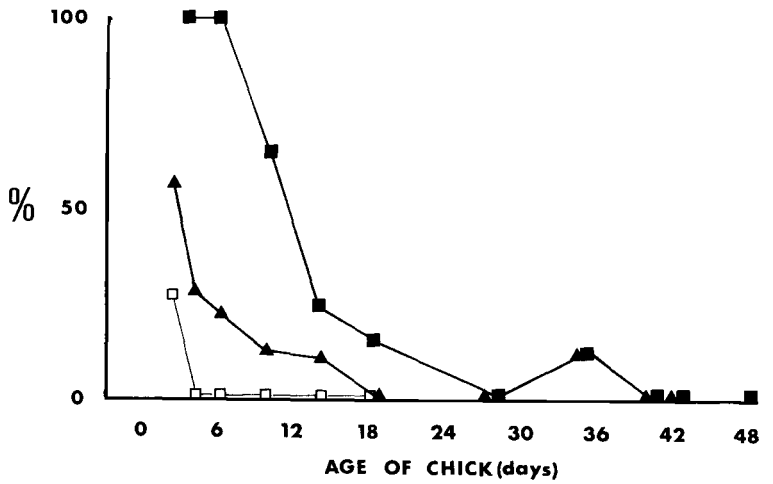

Fig. 4. Percentage of feeding failures for each prey group in relation to age of young (1982 data only). Open square: small and shallow-bodied fish (sandlance, gunnel); triangle: intermediate-sized fish (herring, smelt, cod, prickleback, unidentified); solid square: large, deep-bodied fish (shiner perch).

the group with the greatest depth and body weight (seaperch) the week before chicks fledged. Because adult loons are able to carry heavier fish than we observed (for example, see Norberg and Norberg 1976) and prey size approximated the swallowing capabilities of the young, size selection by the adults, at least near hatching, may be operating. This could reflect prey availability in the marine habitat rather than parental foraging decisions, although at an additional nest site (1983, unpubl. data), at which the hatch date was 6 weeks earlier in the season than at the 1982 nest, comparable shifts in prey species over time were observed.

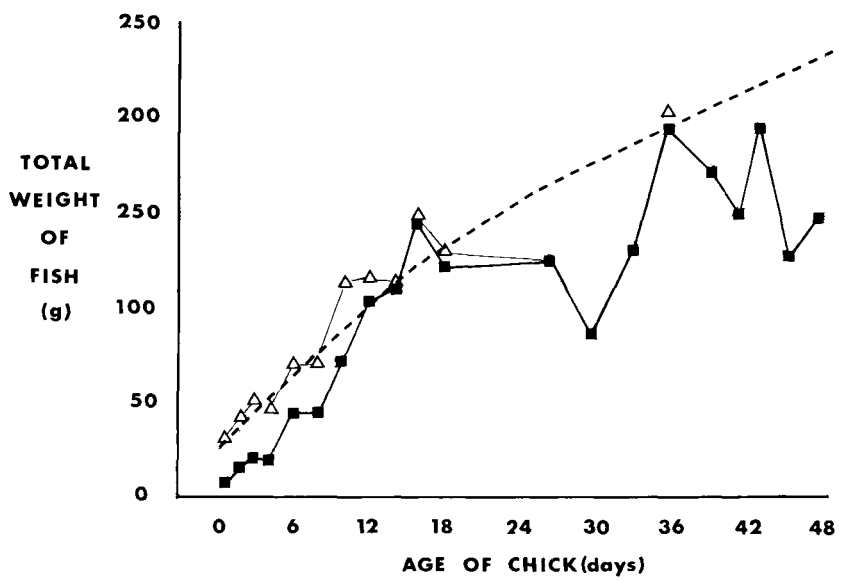

Fig. 5. Daily weight (g) of fish eaten by young in relation to age of young (1982 data only). Solid square: actual food consumption by young; open triangle: total weight of fish brought by adults; dashed line: daily food requirements predicted from existence energy. Values for fish brought and consumed for Days 1–13 were calculated for single chick on the assumption that both chicks were fed similar amounts.

Of 28 fish fed to the chick during the first 2 days, 82% were small (sandlance and gunnel); the proportion of these dropped to 34% from Day 3 to 6 and to 6% over the rest of the prefledging period.

Fish brought to the young are occasionally too large for the young to swallow (Pearse 1946, Rankin 1947, Davis 1972), yet such failures represented only 4% of all observed feedings in this study. There should be a selective advantage to bringing fish at the upper size limit of the swallowing capabilities of the young. A 1,000-g chick would require about 200 g of fish per day (Junor 1972); if sandlance were the only fish in the diet (est. weight 1.5 g), daily food requirements could not be met, because average return flight time to the ocean is 60 min and total daylight at this latitude is 18 h. By bringing seaperch (22.5 g), adult loons meet chicks' requirements in nine flights. The ability of the adults to bring chicks sufficient food appears to be more critical early in the prefledging stage, when daily weight is comprised of numerous small fish rather than a few large ones.

Fish were regularly dropped and occasionally regurgitated by chicks during manipulation and were retrieved from the water by the adults, a behavior also observed in Common Loons and Yellow-billed Loons (*G. adamsii*) (Sjolander and Agren 1972, 1976). Even when the caudal fin protruded from the chick's bill after it had swallowed the fish, the parents dove repeatedly. This redundancy, which would insure that prey was utilized, is probably functional, because the energy investment in feeding flights is high (Norberg 1981).

Junor (1972) determined that the daily food consumption of hand-reared *Phalacrocorax* and *Ardea* species ranged from 50% of the body weight after hatching to 16% near fledging. Using existence energy and costs of growth and activity in prefledged birds, Wiens and Scott (1975) predicted similar values. In our estimates of daily food consumption, observed values for Days 10–18 were similar to predictions but were 10–50% lower during early and late prefledging periods. Some of these differences could reflect an underestimation of fish weights, given the possible errors in the use of photographic techniques. Alternatively, food (vegetation and possibly fish) obtained by the young during occasional foraging in the lake could account for some of the discrepancy.

Despite the prevalence of fish in the nesting territory, marine fish predominated in the diet of the young (see also Bundy 1976). There would appear to be an immediate selective advantage to the use of freshwater prey, because, during adult foraging flights, the risk of predation on unattended chicks may be high (unpubl. data). There are at least three interpretations of this parental foraging behavior. (1) Red-throated Loons commonly nest on tarns without resident fish and obtain food for the young from the ocean (Johnson and Johnson 1935, Davis 1972, Bundy 1976, Furness 1983) or, in interior Sweden, from larger lakes (Norberg and Norberg 1976). The species may be genetically and behaviorally committed to foraging away from their nesting lake (Sjolander pers. comm.). (2) Marine species contain higher levels of trace elements and vitamins (boron, bromine, iodine, lithium, strontium, copper, ascorbic acid, pyridoxin, and niacin) than do freshwater fish (Love 1970). There also may be greater foraging predictability in the marine habitat during the periods when characteristic size classes are required for the young. (3) An advantage of feeding marine fish to chicks could be the circumvention of the life cycles of freshwater parasites that have both bird and fish hosts (see Dogiel et al. 1958, Olsen 1974). In small bodies of water, where Red-throated Loons generally nest, the parasite load could become exceptionally high if the young were fed infected fish from the nesting lake. Common and Yellow-billed loon chicks should also be susceptible to infection, because they are fed freshwater fish from the nesting territory, but these species breed on larger oligotrophic lakes (Palmer 1962) where the dilution factor would be much greater and the probability of infection reduced (J. C. Holmes pers. comm.).

In summary, while Red-throated Loons at Drizzle Lake display adaptations that minimize the number of foraging flights, such as returning with prey near the optimal size, the virtual exclusion of freshwater fish from the diet of the young remains problematic in interpreting foraging strategies of the species.

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