Triphasic Feeding Behavior and the Esophageal Diverticulum in Redpolls

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Most adaptive characteristics of redpolls (*Acanthis* spp.) are keyed to surviving an arctic or subarctic winter, where energy balance is the severest problem. Many features combine to produce the total adaptation that makes these tiny birds some of the most cold-hardy of homeotherms (Brooks 1965, Ph.D. thesis, Univ. Illinois, Urbana), but the presence and specialized use of the esophageal diverticulum may be among the most important. It is a partially bilobed, ventrolateral outpocketing located about midway on the neck, found in redpolls and certain other northern finches (e.g. crossbills, *Loxia* spp.) but absent in most other passerines (Fisher & Dater 1961, Auk 78: 528). The ventral, unilobed "crop" in galliformes and others is only somewhat analogous in structure and function.

The adaptive value of the diverticulum manifests itself in three aspects: (1) "extra" energy gained, (2) energy saved, and (3) reduced predation. Extra food is stored there toward nightfall, carrying the bird through low night temperatures when it is unable to feed. I have estimated that the amount of birch seeds that could be stored in the diverticulum by Common Redpolls (*A. flammea*) and used at night would allow survival to −62°C, a substantial increase in cold tolerance over the −30°C that could be tolerated without that extra energy (Brooks 1968, Wilson Bull. 80: 253).

A hitherto unreported use of the diverticulum is as an energy saving device. During the winter finch invasion of 1971–72 in Ripon, Wisconsin, I observed that individual redpolls hurriedly selected millet from the seed mixture at a feeder, then flew away. This produced a constant, rapid turnover of the feeding flock. There were never more than about 100 birds feeding, but mark-recapture banding data indicated that 1,000–1,500 different redpolls utilized the feeder daily. Little agonistic interaction was noted while feeding. Individual Evening Grosbeaks (*Hesperiphona vespertina*), however, remained for fairly long periods shelling sunflower seeds, and many intraspecific agonistic encounters were seen. Closer observation showed other differences between the species. Especially on colder days, redpolls ingested seeds rapidly without shelling them. As some individuals ceased feeding they left the flock and congregated in a dense white cedar about 2 m from my observation window. Although they appeared to be resting, plumage fluffed out in the heat-saving "ball" position typical at low temperature, they were actually regurgitating, shelling, and reingesting millet seeds. Due to the numbers processed by each bird I assume these seeds had been held in the diverticulum.

The primary natural food of redpolls is birch seed, about the size of poppy seed. Typical "wild" feeding behavior at first appears distinctly biphasic. The birds, using wings, legs, head, and tail vigorously, spend a short time working acrobatically among the terminal branchlets in phase I, knocking seeds out of the catkins. This muscular activity consumes more energy, and because of the consequent insulation disruption and greater exposure to wind, they lose relatively more calories than in phase II. They spend a longer time in phase II gathering these seeds from the ground (snow, usually) where there is less wind, where they can remain more easily in a ball position, but where they are probably more exposed to the view of predators (on snow). Energy rather than predatory considerations thus may shorten phase I.

Biphasic feeding is already more complex than the feeding of most other birds, but redpoll feeding is actually a triphasic process. In phase III cover is sought and seeds stored in the diverticulum are shelled. This advanced type of feeding behavior, to my knowledge, is unique among birds but is fairly similar to that of the red squirrel (*Tamiascirus hudsonicus*), another boreal treetop harvester. The two obvious benefits of phase III are that additional energy is saved and potential predators are avoided.

The energy saving involves four factors. One is that seeds are undoubtedly softened by moisture in the diverticulum, making hulls easier to remove and allowing easier mastication of the hydrated edible portions in the gizzard. Slightly less energy is expended for this necessary work (though some calories are lost in heating expelled hulls and water), and more is thus available for body heat production or other activities. This hydration phenomenon is quite reminiscent of cud-chewing in ruminants, whose stomach compartments allow proper separation of processed from unprocessed food. It is probable that the need for efficient separation is the reason that the esophageal pouches in redpolls are laterally oriented. The question has been raised (Fisher & Dater op. cit.) as to why the diverticulum is not ventral as the crop is in galliformes. If it were, ventral gravity would disallow easy separation of shelled seeds on their way down from unshelled ones on their way up. They would be thoroughly mixed and much time and energy would be wasted moving them in the improper direction. Those species having a ventral crop do not encounter this problem since they do not regurgitate and shell seeds. Lateral crop placement thus puts major emphasis on sorting and retrieval, not simply storage. It supports the idea that the function of the diverticulum is not only to hold extra food but also to aid in the general saving of energy.

A second factor in the saving is that because fewer birds are present on the feeding area at one time, direct competition is reduced. Less energy is expended superfluously in aggressive encounters, and more can be directed toward feeding.

Third, the least disruption of plumage (insulation) due to feeding occurs if a bird is not repeatedly raising and lowering its head to pick up and immediately shell seeds. If shelling is done elsewhere, the head can remain down when gathering seeds, and then kept horizontal when shelling them. Thus the insulation layer always can be maintained as perfectly as possible, and there is lower net heat loss.

The last factor is probably the most important. Energy saved by being in a cavity is quite great (Kendeigh 1961, Wilson Bull. 78: 140). Dense coniferous foliage, used preferentially as cover by redpolls, approximates a cavity. By shelling seeds here rather than in the open, considerable energy may be saved.

Using the esophageal diverticulum in a triphasic feeding process allows redpolls to save a probably significant (but perhaps unquantifiable) amount of energy, thus increasing their operating efficiency. Due to increased shelling time per calorie gained, the relative saving in phase III increases with selection of smaller seeds, normal for redpolls when not obliged to come to feeders. This extends the importance of the diverticulum beyond merely being a receptacle for extra energy. Both functions lower the limit of temperature tolerance significantly for redpolls under natural conditions, and the birds probably gain the added benefit of reduced predation as well.—*Received 15 January 1976, accepted 14 October 1976.*

Aggressive Display in the Common Loon

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In the Common Loon (*Gavia immer*) intraspecific aggression is vocally communicated primarily by the yodel call. In typical territorial confrontations, the yodel is given from a low crouch position; during flock activity, the yodel is also given from a stationary upright posture in which the wings are cocked and extended horizontally (Rummel and Goetzinger 1975). The form, occurrence, and significance of the crouch posture have been discussed at length (Rummel and Goetzinger 1975), and similar postures have been reported for other *Gavia* species (Dunker 1975). The upright yodeling position, however, has been generally overlooked or unobserved, and its importance as a major signal has not been recognized. As yet, similar postures apparently have not been found in other species of loons (see e.g. Lehtonen 1970, Dunker 1975). In his description of Common Loon "copulatory behavior," Southern (1961) mentioned an upright position, and Yeates (1951: 142) may have been referring to the upright yodeling posture in his description of pairs racing with wings arched and necks low-outstretched, which he interpreted as threat and greeting behavior. However, since in an earlier reference to the same experience Yeates (1950) treated wing-arching and neck out-stretching as separately performed postures, in none of these references were any vocalizations associated with the behaviors, and the descriptions better fit other movement patterns such as penguin-dancing (with wings spread) and swim-flying (rushing) races or stretching and neck-raising (e.g. when greeting), it seems likely that both Southern and Yeates observed other typical loon behaviors and not the upright yodeling posture. In this paper, the Common Loon's upright yodeling position, here called the "vulture" posture to distinguish it from other vertical positions (e.g. penguin-dancing), is described and interpreted, encounters in which it is performed are discussed, and motivation for its performance is suggested.

A population of nine territorial pairs and several resident and transient individuals was studied at Press Lake, 42 km NNE of Ignace, Ontario, Canada, from 22 May to 14 October 1974. The observation period covered pre-nesting, copulation, nesting, incubation, hatching, and flocking activity. The population was divided into three sub-units, varying in size, relative isolation from human disturbance, and amount of observation: in the primary and most isolated sub-unit, 5 contiguous pairs and 3 singles were observed daily from pre-dawn until dark; in the secondary sub-unit, 2 neighboring pairs were studied every 3–4

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