

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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days; and in the tertiary sub-unit, 2 other pairs with territories on main motorboat routes were surveyed once every 3 weeks. With the exception of the information on nesting and chicks given in the *Limitations* section, only data from the primary sub-unit sample are reported.

Description of the upright yodeling "vulture" posture.—The upright yodeling or "vulture" posture may be described by three defining characteristics: (1) the head and neck extended rigidly forward, at an angle roughly parallel ($<40^\circ$) to the water; (2) the body raised and thrust forward; and (3) the wings lifted and arched, with the wing plane at an angle of $<45^\circ$ to the water (see Fig. 1B). Visually, the posture resembled the threat stances of the Cathartidae.

In 30 separate incidents, 44 performances of the vulture posture were observed. The vulture position was assumed by one loon as it was yodeling at another. In most cases, a displaying loon remained relatively motionless until completing the call. In two cases, however, the neck and head appeared to undulate vertically 2–3 times; in four performances, the body was rotated toward or away from an opponent; and twice, while maintaining the basic vulture posture, the displaying loon moved a short distance (<2 m) toward another bird.

Aggressive display and behavior.—The vulture posture occurred only in close quarter confrontations, where opponents were less than approximately 2 m apart. At greater distances, the aggressive crouch position was assumed. After 18 of 20 observed intraspecific fights (contact, lunging, pecking, wing-buffeting), one or both opponents immediately assumed the vulture position and yodeled. In 21 performances of the vulture when the distance between antagonists increased to beyond about 2 m, yodeling loons settled into the crouch position. In two instances, crouching loons shifted to the vulture posture while yodeling when antagonists approached to within about 2 m. The yodel was the only vocalization given concurrently with the vulture posture, and we never observed the vulture posture without the yodel.

From the consistent association of the vulture posture with fighting, the crouch position, and the yodel call, the vulture posture's basic hostile message (in the sense of Smith 1968) was apparent. The relationship between interantagonist proximity and the vulture and crouch postures, the differences between the two postures in amount of energy expended (see Recher and Recher 1969) and degree of uprightness, and the sequential relationships between the vulture posture and fighting and the vulture and crouch positions suggest that the crouch and vulture postures indicate different levels of intensity of aggression and form a graded display: the crouch is a low-intensity aggressive behavior and the vulture is a high-intensity aggressive behavior. Intermediate postures apparently reflect intermediate states of moderately intense aggression.

Confrontations.—The vulture posture was seen from mid-May to early September. Although most territorial disputes were resolved by crouch-and-yodel challenges across boundary lines ($N = 31$), in three additional territorial incidents one particular successful pair invaded the territory of a neighboring unsuccessful pair and close range confrontations involving vulture posturing resulted. The unsuccessful pair eventually relocated and, although often observed travelling through their abandoned territory, did not defend it thereafter.

Ninety percent of the vulture posturing occurred in nonterritorial contexts. Approximately 73% took place during the post-laying social flocking season (roughly 20 June to 8 September), when territorial allegiance gradually declined and unmated loons, unsuccessful pairs, and some successful males (Barr 1973: 131–132) congregated in neutral areas. Typically, two opponents squared off with vulture posturing and yodel calling, or one vultured and yodeled point blank at a less aggressive target, while others looked on. After a few moments of aggressive display, one of the opponents usually retreated by swimming, diving, or swim-flying away. Generally, victors initiated vulture posturing and were more erect while displaying, sustained posturing longer, and displayed more directly than defeated opponents. These characteristics were probably related to the strength and purity of aggressive motivation.

The following incident was typical of many of the encounters in which the vulture posture was performed: on 7 July, a group composed of two singles and an unsuccessful pair formed in a neutral area. After introductory ceremonial behaviors, one of the singles dived and left the group. The three remaining loons drifted apart momentarily, then regrouped and agonistically circled several times, accelerating the rapidity and jerkiness of peering and other movements. Suddenly the single and one member of the pair splash-dived and abruptly surfaced in a fight, with noisy splashing and wing-slapping. The third bird (the other member of the pair) did not appear to participate actively, but swam slowly about 3 m away (Fig. 1A). The two combatants quickly separated to a distance of about 1.5 m. One antagonist, positioned between the onlooking third bird and the other combatant, assumed the vulture posture and yodeled at the other opponent, which had resumed the normal swimming posture (Fig. 1B). The winning antagonist maintained the vulture position and yodeled until its opponent had rushed 2–3 m away (Fig. 1C); then it stretched and settled into a moderately alert posture close to and facing the onlooker, which had moved slightly toward it. The onlooker went from its moderately alert posture to a low drifting pose, and both

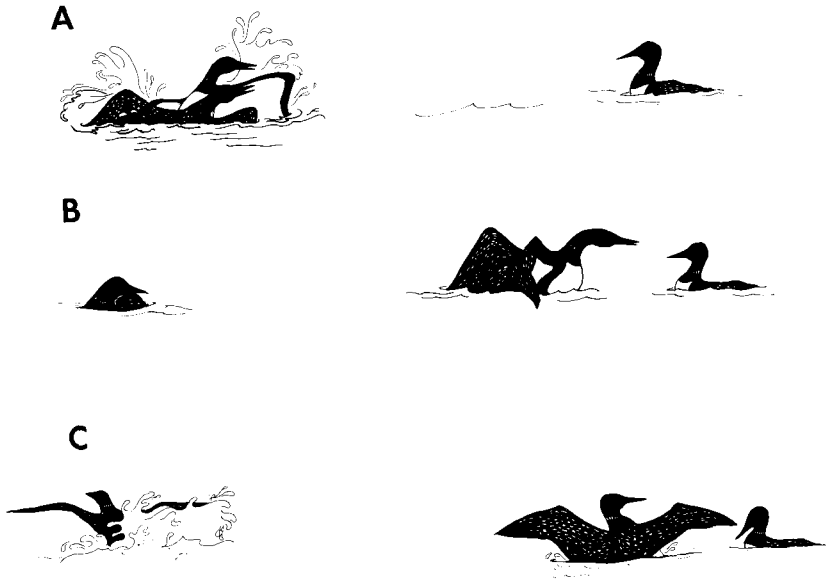


Fig. 1. Vulture posturing and yodeling in a triadic interaction, 7 July in a neutral area. A. After splash-diving, a fight erupted (at left) between a single and one member of a pair. Both combatants were probably males. The other mate (presumed female) drifted nearby. B. One combatant backed down and returned to a normal swimming posture; the other opponent, later identified as the onlooker's mate, continued to vulture and yodel. Its mate continued to drift nearby. C. The retreating bird swam-flew off. The remaining opponent stretched and swam off with its mate to their territory.

mates returned to their territory. The victor swam slowly, slightly ahead of the onlooker, with neck raised and curved, breast exposed, and bill tipped above the horizontal; its mate swam with neck less curved, breast less exposed, and bill tilted downward (see fig. 2 in Tate and Tate 1970).

Several aspects of close quarter confrontations indicate that sexual rivalry between males over nearby females may be a major motivation for fighting and aggressive display: (1) In eight definitive cases, the pre- and post-confrontation swimming postures of mates (identified by their emergence from or return to specific territories) matched certain sex-related behaviors observed by Tate and Tate (1970); from this, we inferred that the aggressors were males and the onlooking nonparticipants were females. (2) In seven other incidents, an unidentified nonparticipant paired up and swam off with one of the displaying loons. (We did not see any case where opponents paired up after close quarter confrontations.) In eight cases, an onlooker approached an antagonist and stayed near it during the confrontation. These observations suggest that for onlookers, the vulture-and-yodel may be sexually significant. (3) Two members of two different pairs displayed idiosyncratic characteristics ("jerky" swimming and "coarse" wailing) by which they could be identified. In the six hostile encounters in which these individuals could be recognized, each individual always performed the same role. And (4), in four clear-cut cases, an onlooker was separated from one antagonist by the other in what may have been a strategic defensive/possessive maneuver. In addition, the interpretation of sexual rivalry is consistent with the observation that fighting may occur between *G. arctica* males when a strange and single male persistently approaches a mated female (Dunker 1975).

Sexual rivalry may not be the only motivation for intragroup hostility. On four occasions, we observed close range confrontations between two unaccompanied loons in the absence of any apparent immediate stimulus for sexual competition. In six other incidents where nonparticipants were present there appeared to be no pairing-up after the confrontation, but a general dispersal of all birds instead. (In five incidents, the outcome could not be determined.) It has been suggested that some confrontations may be due to violation of individual distance (Rummel and Goetzinger 1975). It is also possible that aggressive behavior may be given by a male in the presence of a female as a direct act of sexual dominance or advertisement.

Limitations.—Extensive flooding occurred in the spring in the Ignace area, especially in the English River system, of which Press Lake is a part. Most pairs made several attempts to nest but were flooded

out. By hatching time, nests were as much as 17 m from the shore, separated from the lake by steep grades or dense ground vegetation. Successful egg laying appeared to be directly related to the flood conditions: all chicks in the entire population ($N = 7$, of 5 pairs) hatched 7 July, 29 days after cresting (9 June), and the abandoned eggs of one other pair were known to have been laid on 9 June. (After cresting, no nests were found for 3 pairs.) The flooding introduced an unusually high degree of synchronism in breeding, and, as the occurrence of hostile behavior has been found to vary with stage of breeding cycle (Rummel and Goetzinger 1975), quite likely in aggressive motivation and behavior as well. The pre-nesting period (from the arrival of the loons on 5–6 May [B. Saunders, pers. comm.] to the lake's cresting on 9 June) was 2 weeks longer than the typical pre-nesting state (see Olson and Marshall 1952: 40, Sjölander and Ågren 1972), providing an extended opportunity for contact and prolonging pre-nesting motivation states. Hence, the incidence and intensity of aggressive interaction may have been atypically high.

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Male Pintails Defending Females from Rape

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Hochbaum (1944) applied a classical theory of territoriality to breeding Anatidae. In subsequent studies, however, a closer analysis of behavior and habitat use has revealed a wide variation among species in this tendency (Sowls 1955, Dzubin 1955, McKinney 1965). Among *Anas* species the Pintail (*A. acuta*) seems most divergent. Smith (1968) and McKinney (1973) reported Pintail home ranges broadly overlapped, a high incidence of promiscuous mating, and little defence of females by their mates from raping males. This is in contrast to the much more prevalent male-to-male aggressive behavior displayed by other *Anas* species (Weidmann 1956, Seymour 1974). We present evidence indicating that male Pintails will attempt to defend their mates from rape.