

THE COMMUNICATION OF INTRASPECIFIC AGGRESSION IN THE COMMON LOON

LYNDA RUMMEL AND CHARLES GOETZINGER

THE role of the yodel call in the communication system of the Common Loon, *Gavia immer*, has not been well understood or extensively investigated. Previous studies provide only limited description and discussion of the occurrence and/or social significance of the yodel, and its territorial importance has been noted only briefly. Yeates (1950), studying several Icelandic lakes for two spring seasons, did not observe the yodel; and Munro (1945) did not mention it in his discussion of loon activity in the Cariboo Parklands. Dunlop (1915) described only the auditory features of the call. Olson and Marshall (1952: 24-25) professed the impossibility of describing and interpreting the yodel, but noted several instances of its performance: They reported that the yodel was given during the "reverberating" night choruses and at dusk and night by loons flying in wide circles over other loons on the lake. Further, they wrote that the yodel indicated "annoyance or disturbance" to seaplanes taking off, and reported one occasion where a tremolo (laugh) call "gave way" to a yodel when a pair's territory was intruded upon by humans. Hantzsch (1928) associated the yodel with distress or pain. The yodel was also interpreted as a "love song" (Sim 1923) or reproductive call (Palmer 1962: 25), but reports of Common Loon reproductive behavior (Southern 1961, Tate 1969, Tate and Tate 1970, Sjölander and Ågren 1972) do not indicate that the yodel is related in any direct manner to either courtship or copulation.

Recently, Sjölander and Ågren (1972) sketchily described the yodel as a "territorial marking" that occurred "most frequently during the first phase of reproduction" and was "heard only from owners of territories." Yet despite this current recognition of the territorial significance of the yodel, no account of the call as it is actually performed by loons defending or expanding their territories seems to have been reported. Further, aside from a scant reference by Sim (1923) to head position during yodeling, there appears to have been no mention of any posturing associated with the yodel call. This report presents field observations of the yodel call, a specific "crouch" posture frequently found with the yodel, and the encounters of displaying loons, discussed in terms of the communication and control of intraspecific aggression.

METHODS AND MATERIALS

Observations were made primarily on two different populations of loons. From 20 May to 26 August 1972, eight pairs and four single loons were studied at Catfish

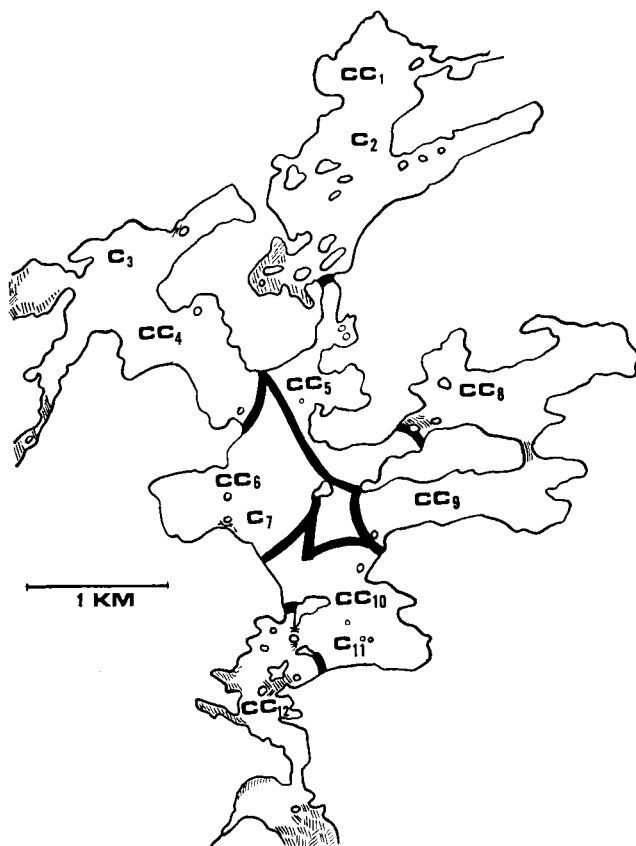


Fig. 1. Cattfish Lake study area. Shading indicates impassable shallow, marshy regions. Territorial pairs are represented by double letters. A single letter stands for a lone loon very often found in the area. Territories are those regions containing double letters and bounded by land masses or impassable areas and dark heavy lines.

Lake in Algonquin Provincial Park, Ontario, Canada (Fig. 1). Of these, seven pairs and two singles were kept under continual observation, while the remaining birds were studied every 3 to 4 days. The lake is on one of the major travel routes in the park and was subjected to heavy small motorboat traffic in the spring and canoe traffic for the rest of the summer season. In contrast, the second population, at Press Lake in the Kenora District of Ontario, consisted of seven pairs and three singles in an environment far more isolated from human disturbance (Fig. 2). From 19 May to 21 August 1973, five pairs and two single birds were continually observed, while the remaining loons were studied at 3- to 4-day intervals. Although other parts of Press Lake were heavily fished in the spring, motorboats completely avoided most of the study region because of dangerous rocks and shallows.

The observation periods covered nest building, incubation, hatching, and mid-

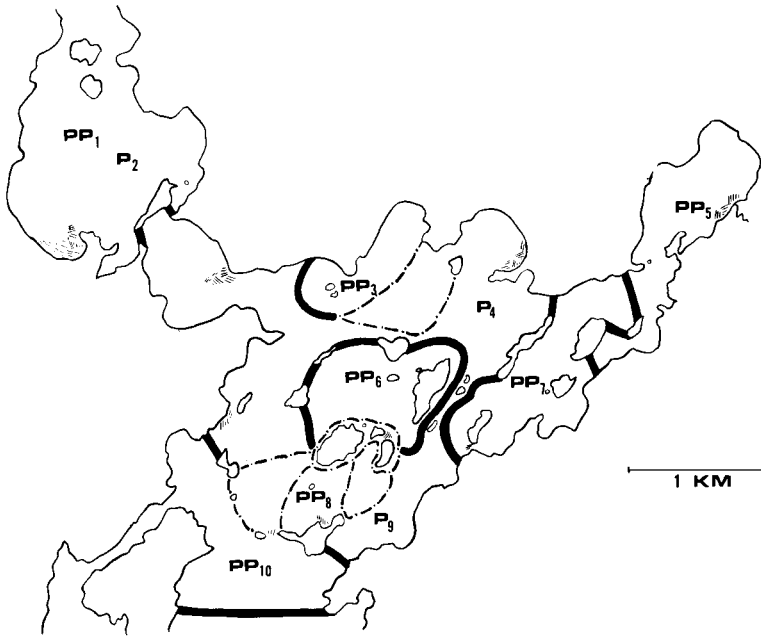


Fig. 2. Press Lake study area. The two clusters of dotted lines near the center of the map depict the territorial expansion that occurred over the summer season by successful pairs PP₃ and PP₈. The small space around the letters is the core nest area defended by the pairs prior to the hatching of their chicks. Near hatching, these areas were enlarged through agonistic encounters with neighboring pairs.

July and August social season flocking. During these periods, we lived unobtrusively in the study areas, except for day-long trips out for supplies every 2 or 3 weeks. This method of continual, intensive study of moderately sized populations permitted us to be reasonably certain of the identity of individual loons and pairs, to place their behavior in meaningful context, and to maintain relatively complete daily records on the majority of the birds in each population.

Additional observations were made on several lakes in the north central section of Algonquin from 27 July to 26 August 1971, while surveying the region for a suitable study population, and at Cattfish Lake from 19 to 27 September 1972.

Recordings were made with a Uher 4000 Report-L at 19 cm/s. Spectrograms were produced on a Kay Electric Co. Sona-Graph 6061-B, using the wide band filter. When possible, observations were supplemented with 16-mm motion pictures and 35-mm stills.

RESULTS AND DISCUSSION

DESCRIPTION OF THE CROUCH-AND-YODEL DISPLAY

The yodel call appears to be composed of an introductory phrase that seems to be the minimum portion emitted, and additional repetitive

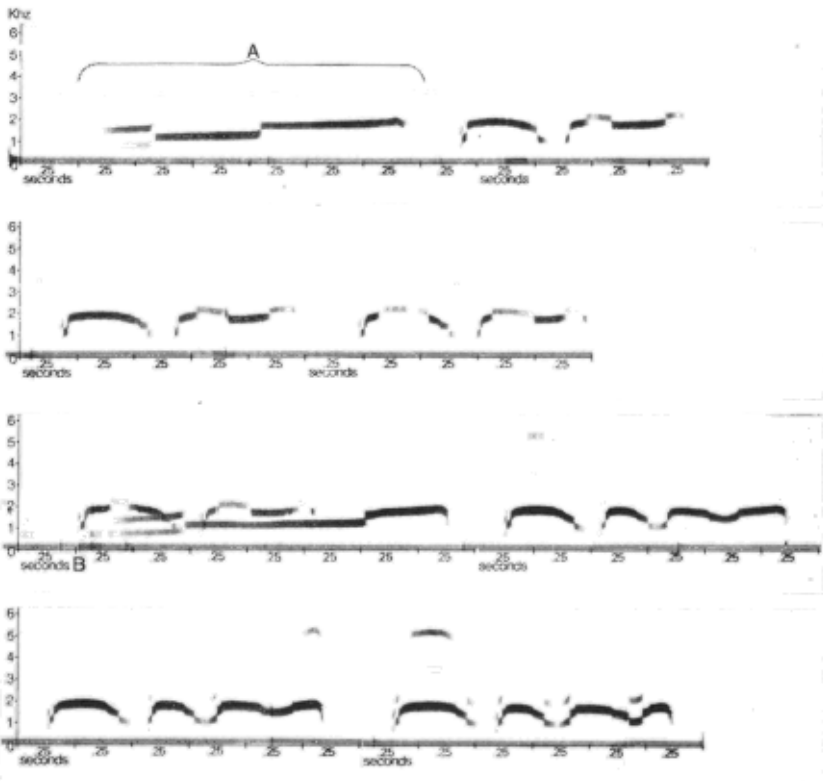


Fig. 3. Spectrogram of two overlapping yodels exchanged in an agonistic encounter between unsuccessful pairs CC_6 and CC_{10} near their mutual border. Each bird gave the yodel while in the crouch position (Fig. 4). A, introductory segment of the first yodel call; B, the contribution of the second yodeler (CC_6) overlaps the call of the first (CC_{10}). Note consistency within and differences between yodels. 11:10, 28 June 1972.

segments that appear to be more responsive to individual and circumstantial variation (Fig. 3). In conjunction with the call, a crouch posture is assumed: The displaying loon hunches low in the water, neck and head extended horizontally, with the bill tipped up slightly and open when yodeling (Fig. 4A). After vocalizing, the yodeler returns to an alert or moderately alert position (body riding high in the water, neck raised, head high, Fig. 4C). Once the crouch position is taken, the introductory segment of the yodel invariably follows; these appear to constitute the core of the communication event. For simplicity, we refer to this aggressive behavior as the "crouch-and-yodel display."

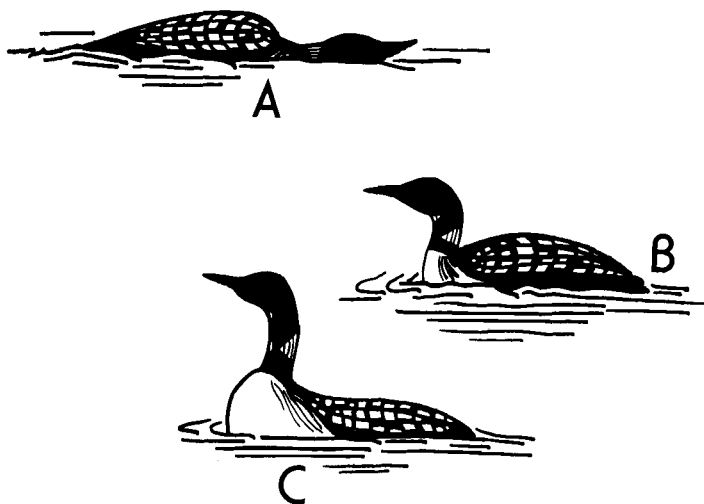


Fig. 4. Postures associated with the crouch-and-yodel display. A, crouch position, assumed when giving the yodel call (Fig. 3). B, moderately alert posture. C, alert posture (raised neck position).

AGONISTIC ENCOUNTERS

The crouch-and-yodel display occurred most frequently in confrontations between two or more pairs near territorial boundaries, especially when one pair trespassed into another's territory (Table 1). Both members of a pair were usually present in boundary confrontations, but sometimes only one mate was involved. In all boundary encounters seen, only one individual of each pair performed the crouch-and-yodel display. The accompanying bird (known to be the mate in most cases) typically remained moderately alert but relatively passive near the yodeler (sometimes in front), occasionally gave low vocalizations (moans and hoots) while the partner was yodeling, and often stretched after the partner's display (various vocalizations and other behaviors are reviewed in Olson and Marshall (1952) and others). In cases where an encounter involved a pair with young, one adult stayed with the chicks, concealing them in a cradle of back feathers or herding them against the far shore, while the other bird confronted and chased off the intruders. We did see one case where a single parent tending the young alone performed the crouch-and-yodel display to challenge a distant pair; hence performance of the display is not restricted to noncaretaking adults. The greater frequency of display performance by the noncaretaker and the fact that only one member of a pair performs the display in an encounter suggest that the crouch-and-yodel display is more typical of one sex than the other,

TABLE 1
BOUNDARY CONFRONTATIONS IN TWO POPULATIONS OF COMMON LOONS^{1, 2}

Successful pair	Antagonist	Encounter dates	n	Hatching date
CC ₁₂ —	CC ₁₀	26, 27, 28 June	3	25 June
PP ₈ —	PP ₆	30 May; 17, 20, 27, 29 June; 1 July	6	26 June
PP ₈ —	PP ₁₀	19, 24, 30 June; 5 July	4	
PP ₃ —	PP ₆	21, 27 June	2	21 June
PP ₈ —	PP ₇	18, 22 June	2	
			Total	17
Unsuccessful and nonbreeding pairs				
CC ₆ —	CC ₁₀	31 May; 2, 17, 18, 21 (2) ³ , 27, 28 June; 3, 5, 8 (2), 9, 18, 20 July	15	
CC ₉ —	CC ₁₀	3, 6, 14, 18, 19 June; 22 July	6	
CC ₆ —	CC ₅	18, 21 June; 8 July	3	
CC ₆ —	CC ₉	5, 14 June; 26 July	3	
CC ₆ CC ₉	CC ₁₀	14, 21 June; 6 July	3	
CC ₆ —	CC ₄	6, 22 June	2	
CC ₅ —	CC ₈	7 June	1	
PP ₆ —	PP ₇	3, 6, 10, 13 June	4	
			Total	37

¹ Confrontations involved one or both members of a pair.

² Data are for continually observed successful pairs (n = 3) and unsuccessful/nonbreeding pairs (n = 9) only.

³ Number in parentheses indicates two encounters on that date.

though perhaps it is not sex-specific. With fair reliability, sexual identity can be ascertained by noting characteristic sex-related variations in the swimming postures of mates (Tate and Tate 1970). Using this method, we were reasonably certain that the male was the displaying loon in eight encounters. We were unable to make definite judgments in other confrontations because of changes in posture, buoyancy, sleekness, and other factors contributing to perceptual distortion. As both parents are known to tend the young (Olson and Marshall 1952: 58–59; Sjölander and Ågren 1972), resolution of this point can come only with certain knowledge of the sex of encounter participants.

Both the territorial defender and the intruder were noted initiating encounter yodeling, but in most cases the occupant appeared to begin the exchange. In many instances, the resident performed the crouch-and-yodel display as soon as the opponent came into view. The defender faced the intruder directly when performing the display. The intruder usually responded with a yodel that overlapped or followed the initiator's call (Fig. 3). Encounters included as many as seven rounds, seldom more, usually fewer. A yodeler sometimes persisted through two or three lengthy yodels without a reply from another loon; a reply, however, seemed to increase the number of calls.

Exchanges were ended by either party. A conclusion typically came when one or both members of a pair dived or began to swim away, although sometimes yodeling continued despite the retreat or disappearance of the intruders. Often termination was preceded by rapid, alert lateral movements of the head and peering. These behaviors also occurred at pauses in encounters and appeared to indicate uneasiness, perhaps a manifestation of conflicting flight and attack tendencies.

Twice we found termination associated with the intervention of another bird not originally involved. On the first occasion (28 June 1972) a lone unmated loon (C_7) appeared near two confronting pairs (CC_6 and CC_{10}) and began tremolo calling (laughing) during a pause in the yodeling. One of the defending loons responded with tremolos. On the second occasion (20 July 1972) C_7 interjected several tremolos while one member of CC_6 was yodeling in response to a challenge by CC_{10} . Both times the tremolos seemed to be related to the termination of the encounter, as no further yodeling occurred, and all participants left the confrontation area.

Except in the core nesting area of successful pairs (see Fig. 2), single unmated birds had relatively free passage through all waters during the territorial season. Lone birds were generally cautious and alert when in another's territory, and usually displayed nonaggressive head movements (quick, low forward thrusts of the head and neck) preliminary to diving and leaving the territory when an occupant was sighted. Single birds appeared to be less cautious with nonbreeding and some unsuccessful pairs, and threesomes were spotted from time to time early in the summer season. For the most part, we were able to identify these triads as involving known pairs and singles; however, it is possible that some of these small groups may have been composed solely of unmated loons and may represent courtship parties or pair formation encounters.

Three pairs were occasionally involved in encounters that occurred at a junction of several territories or included a neutral area. In these confrontations, one of the three pairs was usually involved in only a minor way, perhaps giving only one yodel and not seeming to be the target of either of the other pairs. Interestingly, on two occasions we saw the minimally involved pair return to the boundary a short time after the end of the confrontation and instigate a brief, two-round encounter with one of the other previously involved pairs.

Yodeling was frequently heard in the early season night choruses, in which pairs called from within their territories. In these choruses, loons from distant territories and even different lakes participated in a bout of yodels, indicating that the crouch-and-yodel display (including its initiation) is not dependent on visual contact. During the yodeling, the

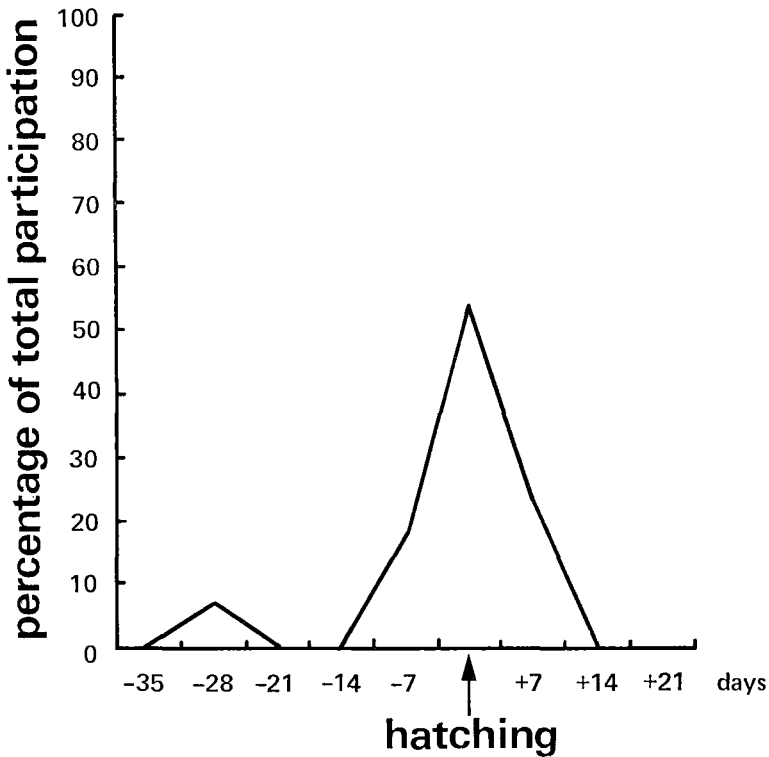


Fig. 5. Boundary confrontations in which successful pairs participated. Data are for continually observed successful pairs ($n = 3$) only. Each pair represented in an encounter was counted once; total = 17. Hatching dates are aligned at mid-interval; days indicate interval midpoints.

other member of the pair often moaned or wailed softly. At least in part, the individual yodeling contributions to the night choruses can be interpreted as aggressive-territorial declarations.

RELATION TO REPRODUCTIVE SUCCESS AND STAGE OF BREEDING CYCLE

Sjölander and Ågren (1972) reported that yodeling was heard most often during the "first phase" of reproduction. We found that performance of the crouch-and-yodel display was apparently related to breeding status and stage of reproductive cycle. In the latter part of June, near the time that their eggs hatched, successful breeding pairs appeared to become more aggressive toward other loons (Fig. 5). This increase in threat behavior appeared to be associated with an expansion in the size of the territories that some successful pairs defended (see Fig. 2). In the early

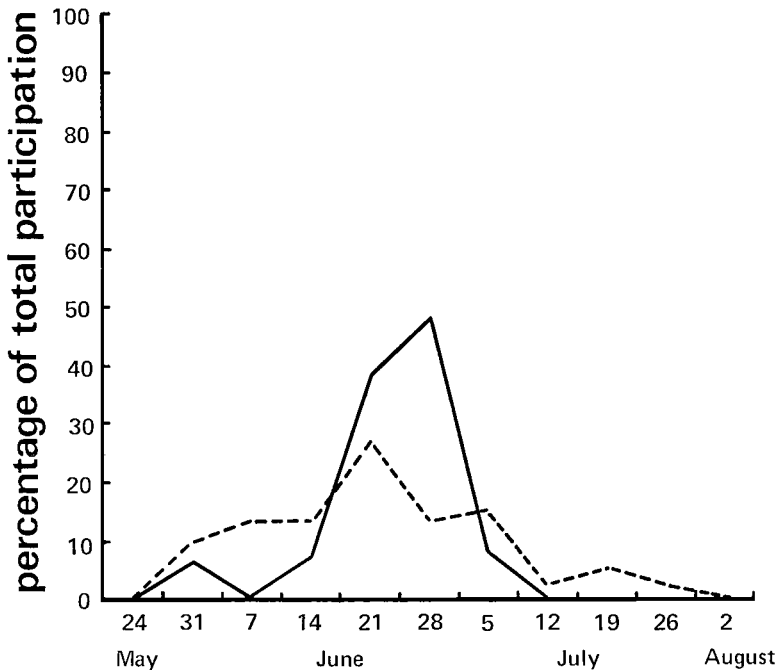


Fig. 6. Boundary confrontations in which successful pairs (continuous line) and unsuccessful and/or nonbreeding pairs (dashed line) participated. Data are for continually observed successful pairs ($n = 3$) and unsuccessful/nonbreeding pairs ($n = 9$) only. Each pair represented in an encounter was counted once; total for successful pairs = 17, for unsuccessful/nonbreeding pairs = 94. Reproductive and social activities occurred on about the same dates for the two main study populations; hence, data for 1972 and 1973 were combined. Dates indicate interval mid-points.

phases of reproduction (egg-laying and the first 2 weeks of the 29-day incubation period), pairs with eggs maintained and defended small core areas around their nests. For example, on 30 May 1973 one member of successful pair PP_8 challenged PP_6 with a crouch-and-yodel display when they trespassed within approximately 40 m of PP_8 's nest. Neither PP_6 nor PP_{10} were challenged when they made frequent patrols past PP_8 's nest area at a greater distance. As hatching approached, PP_8 began to confront PP_6 and PP_{10} aggressively when either pair moved through previously undefended surrounding areas (see Table 1).

Nonbreeding and unsuccessful pairs engaged in agonistic encounters more often in the early part of the season than did successful pairs (Fig. 6). Boundary encounters frequently occurred when an unsuccessful or nonbreeding pair was patrolling. In fact a reliable indication that a

pair was without eggs was patrolling by both birds together during the laying and incubation periods. Patrolling often took place several times a day, and was sometimes maintained until the mid-July flocking season was well underway. Patrolling birds swam slowly and quietly close together along territorial lines in moderately alert posture. This pattern was frequently altered by the pair moving slowly across the frontier into another territory, until they reached some self-determined limit or an occupant appeared. The invading pair often then turned and withdrew, sometimes across the line and sometimes not, while the residents swam rapidly toward them. If the pair stopped retreating or turned to face the defenders, an encounter generally ensued.

The frequency of confrontations for all pairs peaked during the hatching period, but for unsuccessful and nonbreeding pairs this peak reflected encounters initiated by successful pairs. The incidence of territorially motivated encounters dropped off dramatically by mid-July with the advent of the social flocking season and the decline in boundary patrolling. During our entire investigation, we saw only two encounters near boundary lines in August.

NONTERRITORIAL CONTEXTS AND ALTERNATIVE POSTURES

The crouch-and-yodel display also occurred in nonterritorial contexts. It was performed by loons gathered in neutral areas and in the late summer flocks. In these instances, extensive confrontations rarely occurred; instead, one bird squared off against another and, after one or two yodels were exchanged, the participants stretched, preened, and swam away from each other. In the flock, the identity of the antagonists was usually impossible to determine, as confrontations usually took place after many of the flocking loons had dived. Although Sjölander and Ågren (1972) reported that the yodel was heard only from owners of territories, it seems quite likely that the crouch-and-yodel display is also performed by unpaired or transient individuals in aggressive situations, such as when personal space is violated in the flock.

There is some question as to whether the yodel is given only with the crouch position. On a few occasions late in the season, we saw individual loons confronting in very close proximity (within approximately 1 to 3 m) in a flocking area. Although the participants seemed to begin the exchange in the crouch posture, at least part of the yodeling occurred when the loons faced each other with wings cocked and extended horizontally. Olson and Marshall (1952: 24) wrote that in certain circumstances flying loons yodel. We have not seen circling loons yodeling as they described, but we have watched loons on the lake

respond with the crouch-and-yodel display to laughing loons flying over. We have found only the yodel call associated with the crouch position.

RELATION TO THE BILL-DIPPING CEREMONY

On one occasion the crouch-and-yodel display was given in association with the bill-dipping ceremony, a collection of behaviors including bill-dipping, peering, quick (splash) diving, a behavior we called "breast-puffing/bill-tucking," and circling around together (the "circle dance" (Sjölander and Ågren 1972)), performed by two or more loons. On 16 June 1973, two lone loons rapidly approached each other from opposite directions in the territory of an unsuccessful pair (PP₆). One of the birds appeared to be a member of this pair, but the incident may have involved two unmated birds. As they drew closer, they peered frequently; upon joining they began the bill-dipping ceremony. Soon they began to quick dive, sometimes together and sometimes alternating, submerging for only a brief time (at most a few seconds) and surfacing very close to each other. After a few minutes of this, they drew apart. One dived for rather a lengthy time, coming up some distance away, and clearly altering the temporal and spatial patterns that had been established and breaking off the ceremony. This bird dived again for quite some time and surfaced even farther away. While the one was underwater, the other peered and looked around with increasing agitation. The frequency of peering and rapid turning of the head noticeably increased as the length of the other's dive extended. While the first bird was underwater for the second time, the other went into the crouch posture and yodeled toward where the first bird had just been. When the bird surfaced again, the second loon again assumed the crouch position and yodeled. The first loon flew off, leaving the other in an alert pose.

Sjölander and Ågren (1972) suggested that bill-dipping may be a defense reaction to the intrusion of other loons into the territory, or a displacement activity. As we have found territorial defense to be accomplished primarily through the crouch-and-yodel display, the latter interpretation seems more likely, particularly if taken in the sense of a transitional behavior permitting motivational change from hostility to a more positive state (cf. Hinde 1970: 418). Alternatively the bill-dipping ceremony may be regarded as an appeasement activity, a method for reducing the frequency of the crouch-and-yodel display and other aggressive behavior and for permitting relatively close contact among loons. Several aspects of the ceremony and of the circumstances in which it occurs support this interpretation: (1) The behaviors involved in the ceremony appear to be nonaggressive. Specifically, in contrast to the crouch-and-yodel display, there is little prolonged direct frontal orienta-

tion or approach. Participants are usually positioned in parallel or at angles of less than 90° . Performing loons may swim past each other, and much circling typically occurs. (2) The incident described above seems to be a case where the bill-dipping ceremony was performed inadequately and a threatening crouch-and-yodel display resulted. (3) When viewed as an appeasement activity, bill-dipping would be very appropriate as a preliminary to copulation, where, indeed, a highly stylized, synchronized version has been found (Tate and Tate 1970, Sjölander and Ågren 1972). (4) As suggested by Olson and Marshall (1952: 28), bill-dipping does appear to be a greeting behavior. Several times during the early stages of the social season we saw one loon leave a second bird and swim toward a lone loon, engage it in the ceremony, and then return to the second loon accompanied by the other bird. As they joined, hoots were exchanged, and then all three birds gave a lengthy performance of the bill-dipping ceremony. Bill-dipping, with much hooting and circling, also occurred during flock formation later in the season, when loons swam or flew into the group. (5) The ceremony was repeated with considerable regularity among flocking loons, after they had done some fishing, cruising, preening, and perhaps some responsive tremolo calling (laughing). As the ceremony is performed by all participants, it does not appear to be particularly associated with dominance or submission, but is a more or less mutual exchange of signals that minimizes intraspecific aggressive behavior (cf. Marler and Hamilton 1966: 183).

SPECIALIZATION

The crouch-and-yodel display is clearly specialized for the communication of intraspecific aggression. Of the 54 encounters for which we have complete data and the many more we saw or heard, only two culminated in what appeared to be an actual fight. In one of these instances, one member of a confronting pair began by first performing the crouch-and-yodel display, including a number of rapid complete and partial yodels, and then chased after and attacked one member of the invading pair. Further, at no time during our investigation was the crouch-and-yodel display seen given in any situation of interspecific hostility. For example, on two occasions we watched a Common Crow, *Corvus brachyrhynchos*, approach a loon nest as the nesting pair swam nearby. In the first instance (CC₆, 6 June 1972), there were no eggs in the nest. In the second instance (PP₃, 14 June 1973), two eggs had been left momentarily unattended. In both cases, a loon responded to the crow's approach by rapidly swim-flying toward the nest and moaning loudly. Olson and Marshall (1952: 24-25) mentioned one case of a

yodel being given in the presence of human intruders; our experience, however, indicates that this must be quite unusual. Although we have often entered territories and occasionally "threatened" eggs or chicks, we have been met with only quiet retreat, strident agitated tremolo (laugh) calling, or the decoying water-treading display.

Lehtonen (1970: 57) described an aggressive posture for the Arctic Loon, *Gavia arctica*, that appears to be somewhat similar to the Common Loon's crouch position. The male Arctic Loon takes this position just before rushing across the water at a territorial intruder. No particular calls were mentioned in association with this posture, and in contrast to the Common Loon's crouch-and-yodel display, it does not seem to be ritualized. Rather, it appears to be an active prefighting position. Sjölander (1968: 91) described a ritualized threat display in the Arctic Loon, but the "hotdans" (threat dance) seems to differ considerably from the Common Loon's threat display in that the "hotdans" posture appears similar to the alert neck-raised position of the Common Loon.

ACKNOWLEDGMENTS

This research was supported in part by a State University of New York Research Foundation Faculty Research Fellowship and a grant from the State University of New York, College at Geneseo Research Council. We wish to express our appreciation to R. D. Strickland of the Algonquin Provincial Park Museum for his cooperation and assistance, and to T. W. Hueston, District Ranger, for permission to work in the park. Several others working for the Ontario Ministry of Natural Resources were most helpful. Special thanks are due to J. F. Barr, formerly of the University of Guelph, who very generously shared with us many of his own observations on the Common Loon. Lastly, we wish to express our gratitude to Gus, who knew, all along, what the birds were "saying."

SUMMARY

Field studies show that the Common Loon's yodel call is performed concurrently with a previously undescribed crouch posture, constituting a ritualized aggressive display (the "crouch-and-yodel display") typically associated with territorial defense. Boundary encounters and other situations in which the crouch-and-yodel display is performed are described. For successful pairs, performance of the aggressive display seems to increase sharply as hatching approaches; but unsuccessful and non-breeding pairs engage in agonistic encounters throughout the territorial season. The bill-dipping ceremony is interpreted as an appeasement activity that has a significant role in controlling the occurrence of intraspecific aggressive displays.

LITERATURE CITED

- DUNLOP, E. B. 1915. Notes on the Great Northern Diver. *Brit. Birds* 9: 142-147.
- HANTSZCH, B. 1928. Contribution to the knowledge of the avifauna of north-eastern Labrador, part 2. *Canadian Field-Naturalist* 42: 87-94.
- HINDE, R. A. 1970. *Animal behaviour*, second ed. New York, McGraw-Hill.
- LEHTONEN, L. 1970. [Biology of the Black-throated Diver, *Gavia a. artica* (L.).] *Ann. Zool. Fennica* 7: 25-60.
- MARLER, P. R., AND W. J. HAMILTON, III. 1966. *Mechanisms of animal behavior*. New York, John Wiley & Sons.
- MUNRO, J. A. 1945. Observations of the loon in the Cariboo Parklands, British Columbia. *Auk* 62: 339-344.
- OLSON, S. T., AND W. H. MARSHALL. 1952. The Common Loon in Minnesota. *Minnesota Mus. Nat. Hist. Occ. Pap.* No. 5.
- PALMER, R. S. (Ed.). 1962. *Handbook of North American birds*, vol. 1. New Haven, Connecticut, Yale Univ. Press.
- SIM, R. J. 1923. The Common Loon. *Bird-Lore* 25: 167-175.
- SJÖLANDER, S. 1968. [Observations on the ethology of the Black-throated Diver (*Gavia arctica* L.).] *Zool. Revy* 30: 89-93.
- SJÖLANDER, S., AND G. ÅGREN. 1972. Reproductive behavior of the Common Loon. *Wilson Bull.* 84: 296-308.
- SOUTHERN, W. E. 1961. Copulatory behavior of the Common Loon. *Wilson Bull.* 73: 280.
- TATE, J. D. 1969. Mating of the Common Loon. *Proc. Nebraska Acad. Sci.* 79: 50.
- TATE, D. J., AND J. TATE, JR. 1970. Mating behavior of the Common Loon. *Auk* 87: 125-130.
- YEATES, G. K. 1950. Field notes on the nesting habits of the Great Northern Diver. *Brit. Birds* 43: 5-8.

Department of Speech Communication, State University of New York at Buffalo, Buffalo, New York 14226, and Department of Speech Communication, State University of New York at Geneseo, Geneseo, New York 14454. Accepted 15 April 1974.