GRADED FREQUENCY VARIATIONS OF THE TREMOLO
CALL OF THE COMMON LOON (*GAVIA IMMER*)

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The temporal and frequency characteristics of bird vocalizations have been shown to serve in identifying species and individuals. Presumably, stereotyped structural properties encode species information while more variable features are used for individual recognition (Marler 1960, Brooks and Falls 1975). Very few examples are known, however, of consistent species-specific structural variations that have a significance in communication. When these occur, they provide a means of grading the information potentially available in the signal. For example, the addition of harmonics to the duck call of the European Blackbird (*Turdus merula*) indicates an increased probability of taking flight (Andrew 1961). Other examples of vocal signals that are graded by variations have been reported by Konishi (1963), and Berger and Ligon (1977).

The vocal repertoire of the Common Loon (*Gavia immer*) consists of four calls: the tremolo, wail, yodel and the hoot. The tremolo, or laugh, is a highly graded vocalization in which differences in frequency code the intensity of the signal. The purpose of this paper is to describe these variations and how they are used.

The graded features of the Common Loon's tremolo have not been reported in any detail and there is also some confusion concerning the function of the call. Olson and Marshall (1952) described the tremolo as three to eight or ten notes uttered rapidly, and summarized the function of the call as all-purpose, ". . . registering alarm, annoyance, worry, greeting, and courtship." They reported the call as given most frequently when a pair's territory was invaded by an intruder. Rummel and Goetzinger (1975) presented considerable evidence, however, that it is the yodel call that is most often associated with territorial encounters, and the tremolo, when given in a territorial context, "seemed to be related to the termination of (these) encounters." Sjölander and Ågren (1972) also referred to the yodel as the territorial call, and noted that the tremolo was given in "all situations of agitation."

Olson and Marshall (1952) are the only authors to describe frequency variations in the tremolo. They reported the call given as either medium- or high-pitched, depending on the individual and the purpose of the call (there was no mention of how this was determined). They also described a lowering in pitch as the excitement of a territorial encounter diminished. Dunlop (1915) observed that the pitch of the female's wail call was higher than that of the male, but he did not discuss similar differences in the tremolo. Olson and Marshall (1952) stated that determination of the sex of a loon in the field was probably impossible (though Tate and Tate [1970] have since described sexual differences in a swimming posture), and noted that there was no consistent relationship between the size of a bird and the pitch of its call.

Sjölander and Ågren (1976), in their report on the Yellow-billed Loon (*Gavia adamsii*) of Alaska, described a call they referred to as a tremolo that is similar to, but lower in pitch and slower, than that given by *G. immer*. They also noted that the male's calls were slightly lower pitched than those given by the female.

METHODS

I watched and recorded a population of loons primarily from the Roach watershed region of Piscataquis County in north central Maine. The study covered the three breeding seasons from 1974 to 1976. Observation time totaled 715 h with an additional 185 h spent waiting to record individual calls and choruses at night.

The Roach Ponds (Fig. 1) vary in their accessibility to campers and fishermen, and although loons become somewhat accustomed to boat traffic and other human activity, their behavior is affected to some extent by these disturbances. First Roach Pond, the most easily reached, is fished heavily (approximately 20 to 25 boats per week) during the early spring and fall; Second Roach, where most of the data were gathered, averaged nine boats per week. The other ponds are relatively remote and are visited only infrequently.

The six ponds in the study area supported ten pairs of territorial loons and a number of unmated individuals. I spent little time observing the pair in the northwest section of First Roach because of boat traffic there, but observations and recordings were made at each of the other nine territories. At the beginning of the study I made my observations from blinds, but later stopped because the blinds appeared to disturb the birds more than an observer sitting quietly but unconcealed near the shore.

The sex of the loons was determined in two cases (2REP and 2RWP) by identifying the member of the pair that laid an egg. For both of these pairs only the male gave the yodel vocalization, and, since only one member of each of the other pairs gave
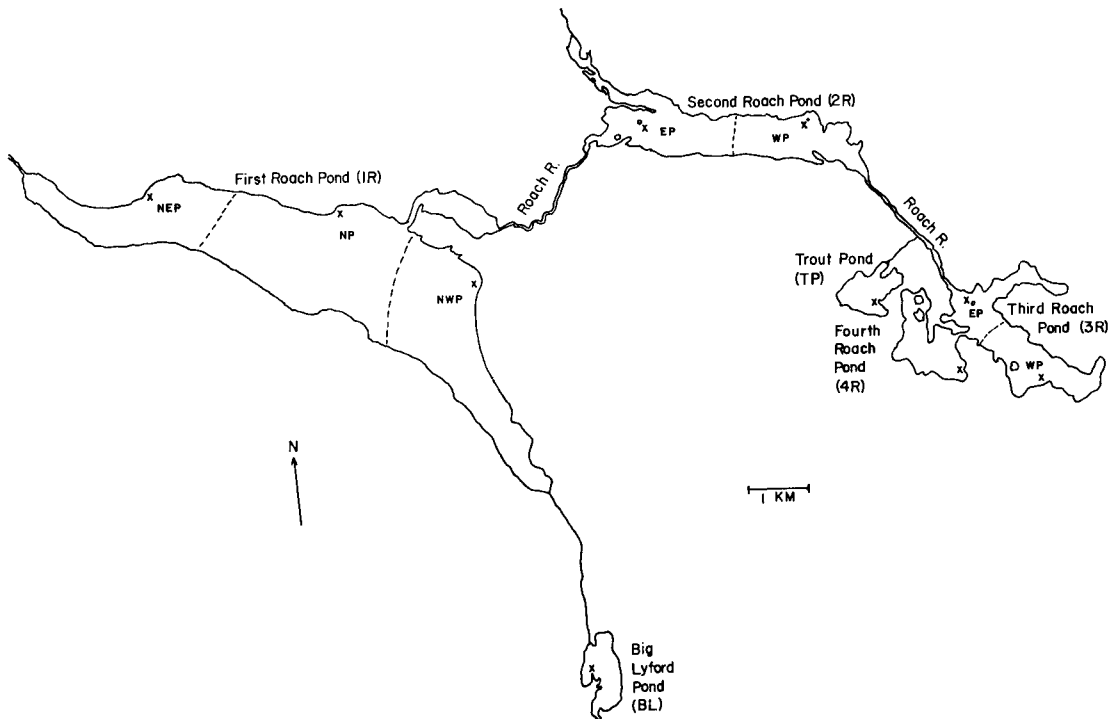
FIGURE 1. Map of the study area. Individuals and pairs are identified throughout the paper by using the location symbols as shown: Second Roach East Pair or East ♂ = 2REP or 2RE♂. The Xs indicate the traditional nest sites, and the dashed lines refer to the general area of the territorial boundaries.

this call, I assumed that a bird giving the yodel was a male. I also attempted to see the sexual differences in swimming posture as described by Tate and Tate (1970). I found that when members of a mated pair are swimming next to each other while patrolling their territory early in the season, there are consistent differences in posture. In other behavioral contexts, however, the swimming attitude varies and is not a reliable criterion for distinguishing the sexes.

Observations were made with a spotting scope and a binocular; notes were dictated into a small cassette recorder and transcribed three or four times a week. Recordings were made on Uher 4400RS and 4000RL recorders at 19 cm per s, with a 48 cm EPM P-500 (electronically equalized) parabolic microphone.

Spectrograms were produced on a Spectral Dynamics Real Time Analyzer. The band width on a real time analyzer is a constant percentage of the analysis range (Hopkins et al. 1974). Because of the relatively low frequency range of the tremolo call (below 1.6 kHz), and the need for accurate measurements of frequency, a low analysis range was chosen. With the tape slowed to one-quarter speed and an analysis range of 500 Hz, the band width is 6 Hz. Frequency measurements were made to the nearest 10 Hz using internal markers at 20 Hz intervals. Selected calls were also filmed at a band width of 60 Hz using an analysis range of 5 kHz. Temporal measurements were made to the nearest 12.5 millisecond by counting the vertical lines produced by the RTA filters, and measurements of the temporal overlap in certain features of the call were taken from spectrograms produced on a Kay Electric Co. Sona-Graph model 7029A at a wide band (300 Hz) setting.

RESULTS

The tremolo call is a relatively slow frequency modulation with a superimposed modulation of amplitude. The mean duration of one rise and fall in frequency (or amplitude) as measured from a total of 40 cycles from 12 individuals was 103 ms, resulting in a modulation rate of approximately 10 cps. The duration of a cycle varies but little (SD = 10) and is, in fact, the most stereotyped feature of the call. The tremolo may begin or end at any point in a cycle and there can be from 1.5 to 10 cycles in a call; so the duration of the tremolo, based on the average modulation rate, can vary from 0.15 to 1.03 s.

The frequency range of a single modulation varies depending on its position in the call; however, because of difficulties in making statistically accurate measurements of the modulation range (attenuation of low frequency side bands in the 6 Hz spectrograms, and poor frequency resolution in wide band), I made few measurements on this feature of the call. Generally, however, the range increases as the call progresses, reaching its maximum (approximately 210 Hz) near the midpoint and then falling towards the end. As the range changes within the call, it does
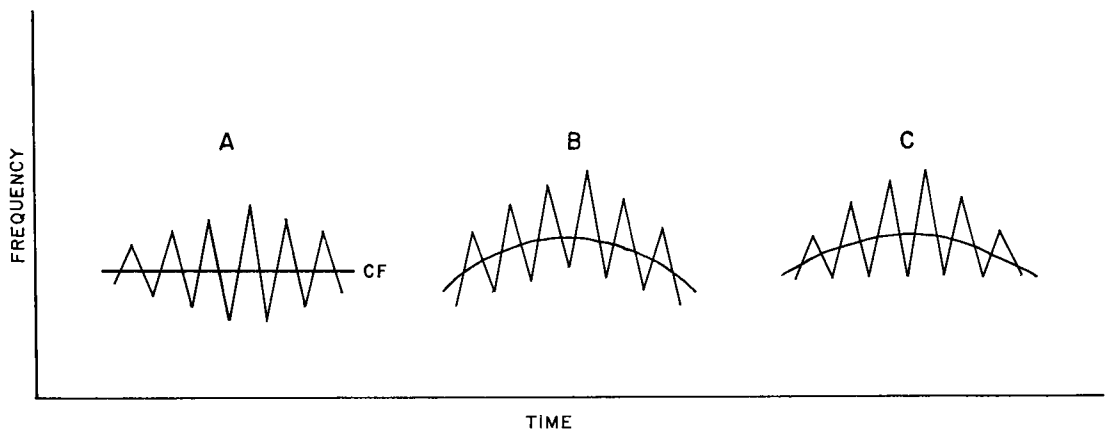
Modulation Forms

FIGURE 2. Three possible modulation forms. The tremolo is given in forms B and C. CF = carrier frequency.

so in a way that allows the carrier frequency to vary with it. Figure 2 shows in a somewhat exaggerated way that this does not have to be the case. Modulation form A increases in range (or in the frequency at the crest of a modulation) with no change in the carrier frequency. The tremolo is given primarily in form B and occasionally in form C; in both cases, the carrier frequency changes with the range. To the human ear a modulation rate of 10 Hz is just at the threshold of resolution (Marler 1969), but assuming that birds have a finer temporal resolution than humans (Pumphrey 1961), it is likely that the loon is able to perceive each modulation as a simple rise and fall in frequency. For this reason, and also because of the difficulties in determining the modulation range, I did not attempt to estimate the carrier frequency of the tremolo. Instead, the frequency at the crest of the modulation was used to estimate the frequency of the call.

The spectrograms produced at the 6 Hz band width represent the call in roughly the way we hear it. Individual modulations are only partly resolved and appear as wedge-shaped stacks of side bands (see narrow band calls in Fig. 3). Higher frequency bands are also emphasized because the amplitude of the call reaches its maximum at the crest of each modulation (Hund 1942). The highest frequency side band is the most easily resolved, and is stable through a wide dynamic range; this band was used to measure the frequency of the call.

CALL TYPES

The frequency of individual modulations of the tremolo call can be manipulated in a complex way to form three different call types. In
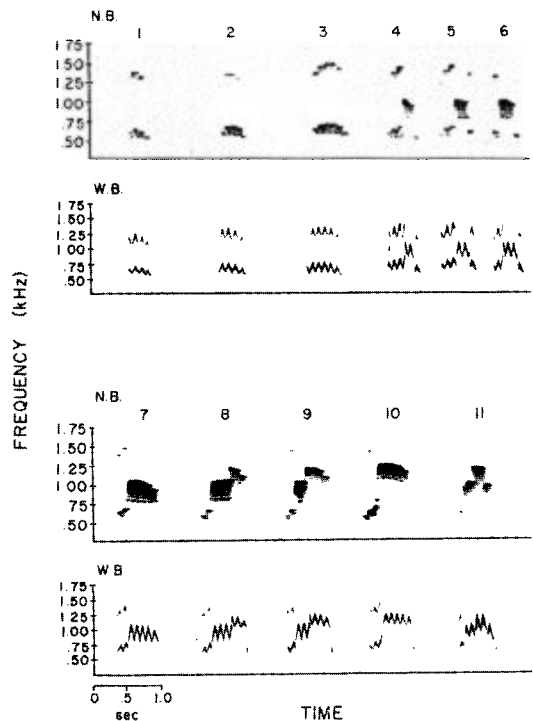

FIGURE 3. Tremolo calls selected to illustrate the three call types and their variations. N.B. = narrow band (6 Hz); W.B. = wide band (60 Hz). The frequency range of the N.B. calls has been expanded somewhat for better resolution of side bands. W.B. calls are tracings. Calls 1, 2, 3 (type 1); 4, 5, 6, 7 (type 2); 8, 9, 10, 11 (type 3).

its simplest form, from 1.5 to 7 modulations form a fundamental with a strong first harmonic (Fig. 3, calls 1, 2 and 3). The frequency of the fundamental varies according to the individual and a number of other factors discussed below, but generally falls between 600 and 800 Hz. This call is referred to as type 1, and frequency range of the fundamental as level 1.

The type 2 call (Fig. 3, calls 4, 5, 6 and 7) begins with one or two introductory modulations in level 1, and continues with a variable number of pulses in level 2, which is approximately one-third of an octave above the first level. The call generally concludes with a return of a single modulation to level 1. The spectrograms suggest that the type 2 call is formed by lifting modulations from the center of a type 1 call, while at the same time slightly increasing the modulation range. Level 2 has no sound energy below it and is itself a fundamental harmonically unrelated to level 1. In fact, close examination of the wide band (300 Hz) spectrograms of some of the type 2 calls shows considerable temporal overlap between levels 1 and 2, suggesting two independent internal sound sources. (See Miller [1977] for a discussion of the two-voice phenomenon.)

The type 3 call is the most complex of the three forms. In general, it appears to be formed from the modulation in level 2 in much the same way that the type 2 call can be thought of as being formed from level 1. If a series of type 2 tremolos is being given with, for example, two introductory modulations in level 1, and four or five in level 2, a type 3 call can be formed by the movement (and reduction in range) of the last one or two modulations in level 2, about one-sixth of an octave higher to level 3. If the total duration of the call remains the same, the length of level 3 can be increased by the progressive addition of the remaining modulations in level 2 (Fig. 3, calls 8, 9, and 10). It can be increased further (with a consequent increase in total duration) with the addition of three or more modulations (the longest type 3 call recorded had nine modulations in level 3). The type 3 call can be concluded in several ways. If the call is relatively brief, there is often a return to the frequency range of level 2 (Fig. 3, call 11) which is very similar to the return of the concluding modulation of the type 2 call to the first level. The call either ends this way, or there may be a final weak pulse in level 1. Longer type 3 calls generally do not return to the second level, but a weak concluding modulation is often present at the first level.

There is much potential for varying the distribution of energy in the three possible frequency levels of the call. Some consistency exists, however, in the occurrence of the introductory modulation with its strong first harmonic in level 1 of the type 2 and type 3 calls. From the total sample of 2,627 type 2 and 3 calls recorded, I found 2,285 in which level 1 was not obscured by background noise or overlap with other calls; of these, 98% had some energy in level 1 at the beginning of the call. The concluding modulation in level 1 is also typically present in type 2 and type 3 calls; although it is somewhat less common than the introduction (89% had a concluding modulation). When a conclusion is present, especially in long type 3 calls, it is generally shorter and less intense than the introduction.

TIME-FREQUENCY RELATIONSHIP

As mentioned above, the length of the type 1 call can vary from 1.5 to 7 modulations. When I measured a sample of type 1 calls from a known individual I found a positive correlation between the duration of the call and the frequency of the highest modulation: the longer the call the higher the frequency. The increase in frequency was due to a shift in carrier frequency with a slight increase in modulation range. The relationship differed for the other two call types. I found little or no correlation between the frequency of level 2 of a type 2 call or level 3 of a type 3 call with total call length, but there was a positive correlation between frequency and duration of the level 2 or 3 segment of each. The lack of correlation between total length and frequency is because the total duration of the type 2 and 3 calls varies less than the length of their respective levels.

Figure 4 shows the time-frequency relationship for 14 individuals. Of the more than 2,800 tremolo calls recorded, I used only 462 to plot the time-frequency slopes; the others were not used either because the identity of the calling bird was not certain, or there was overlap from other calls or too much background noise for accurate measurements. The data points are given for TPδ, but the others have been left out to avoid confusion. In some cases, only one call of a given type could be identified as belonging to a specific individual; these were plotted to give some idea of the frequency range for those birds.

The correlations were all significant ($P < .05$) with the exception of TPδ (type 1 calls, $r = 0.54$) and 1RNW$\female$ (type 3 call, $r = 0.48$). Samples for these call types were, however, small (Table 1).
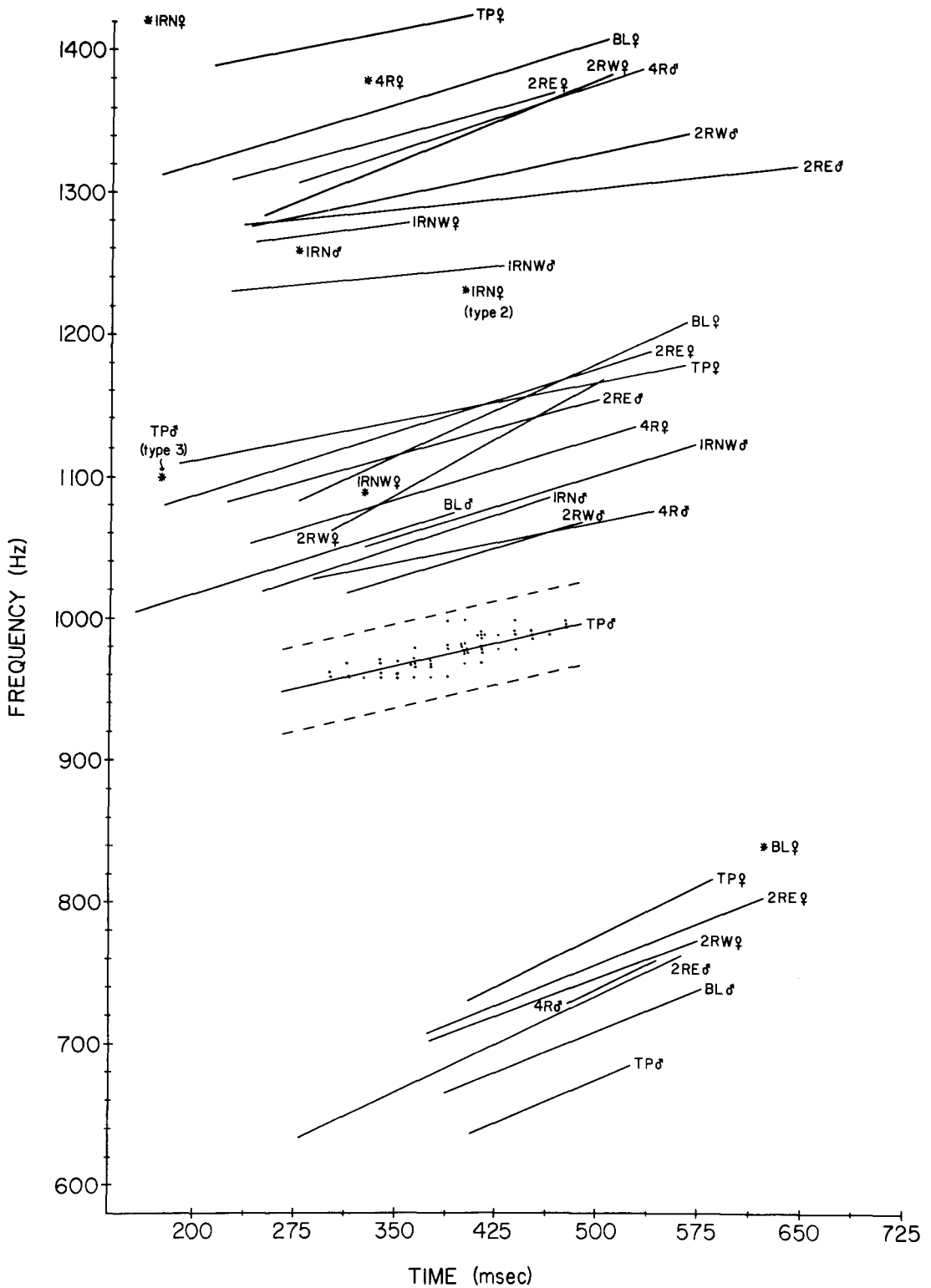
FIGURE 4. Time-frequency relationship for various individuals. The regression lines from 620 Hz to 840 Hz represent the correlation between frequency and the total duration of the type 1 calls. Between 950 Hz and 1200 Hz frequency is correlated with the duration of level 2 of the type 2 calls, and above 1200 Hz the duration of level 3 of the type 3 calls is correlated with frequency. There is some overlap for particularly high and low frequency individuals (see TP ♂ type 3 and IRN ♀ type 2). Dashed lines are the 95% confidence limits for TP ♂ (type 2). * = single calls.

TABLE 1. Summary of data from Figure 4. The slopes and correlation coefficients (r) were taken from measurements of total length vs. frequency for type 1 calls, the length of level 2 vs. frequency for type 2 calls, and the length of level 3 vs. frequency for type 3 calls.

Bird	Type 1			Type 2			Type 3		
	n	slope	r	n	slope	r	n	slope	r
1RN ♂	–	–	–	9	4.03	.69	1	–	–
1RN ♀	–	–	–	1	–	–	1	–	–
1RNW ♂	–	–	–	17	3.74	.74	10	1.23	.72
1RNW ♀	–	–	–	1	–	–	5	1.79	.48*
2RW ♂	–	–	–	15	3.65	.68	51	2.63	.81
2RW ♀	14	4.42	.78	23	7.69	.89	15	5.31	.91
2RE ♂	22	5.40	.95	22	3.14	.90	19	1.53	.85
2RE ♀	20	4.83	.81	15	3.72	.93	14	3.42	.91
4R ♂	12	5.71	.62	8	2.57	.78	8	3.80	.86
4R ♀	–	–	–	10	3.75	.88	1	–	–
TP ♂	5	?	.54*	56	2.35	.83	1	–	–
TP ♀	12	4.32	.93	8	2.26	.85	7	2.98	.87
BL ♂	9	4.87	.95	4	3.71	.98	–	–	–
BL ♀	1	–	–	28	5.37	.74	17	3.62	.89

* Not significant (P > .05).

Most of the calls were recorded during the 1976 season, and were from a variety of contexts. I have too few data as yet to be certain if the context affects the slope of the time-frequency relationship. The data for the three call types of TP ♂ were taken from three different contexts in each of which the type 2 call was given. These calls were then plotted separately for each situation, and the regression lines scarcely differed even though the mean duration of the calls varied considerably in two of the three cases. Four other birds (2RE ♂, 2RE ♀, 2RW ♀, and BL ♀) were recorded in two different contexts each, and although the sample sizes were smaller than for TP ♂, the results were roughly the same. Figure 4, therefore, represents pooled data from different contexts for these individuals.

My limited statistical analysis of the time-frequency data reveals several interesting relationships. For a given individual, the range in peak frequency of the type 1 call is discrete in that it does not overlap the range in frequency at the crest of level 2 in the type 2 call. In the same sense, level 2 is not continuous with the third level of the type 3 call. Overlap would be expected if the duration of a call continued to increase, but the maximum length of the type 1 and 2 calls is evidently limited. From the sample of all recorded calls, the longest type 1, and the longest level 2 of a type 2 call, were 675 and 625 ms respectively. Figure 4 thus represents well the distribution of call length for these two types in the larger sample.

Level 3 of the type 3 call is often consider-ably longer than is represented in Figure 4. Durations of 775 ms are not uncommon and, as mentioned above, the longest type 3 had nine modulations in the third level and measured 825 ms. Long type 3 calls were never recorded during the day, but were often given during social chorusing at night. Since I could not identify individuals with any certainty at night, these calls were not included in Figure 4.

The interval separating the first two levels for an individual bird is roughly 350 Hz, and between levels 2 and 3 approximately 220 Hz. These intervals are affected, however, by the variations in slope between levels; although the differences are small, and not always consistent for a given individual, the slopes tend to decrease progressively from level 1 to level 3 (see Table 1).

The interval between levels 2 and 3 is less than that between the first two levels, and some overlap occurs here between high and low frequency individuals. I found no similar overlap between the first two levels, although this is probably due to the small sample size.

The 95% confidence limit for TP ♂ (type 2 calls) is indicated by the dashed lines. The limits are similar and in some cases wider for the other birds. For a given call type, frequency overlaps greatly for most of the birds, and it is only the individuals at the extremes that one would expect to differ in a statistically significant way. The regression lines of the females, however, tend to be higher than those of the males, although again there is some overlap. This effect is not due simply to the

TABLE 2. Call types associated with the various contexts in which the tremolo was given.

Contexts	Number of incidents observed	Type 1	Type 2	Type 3	Number of individuals whose calls were recorded
Boats	41	102	365	216	24
People on shore	16	13	88	43	7
Seaplanes	8	–	no recordings	–	–
Flock displays	24	27	244	112	27
Resident chase intruder	4	–	15	10	1
Other loon flying over	4	–	no recordings	–	–
Flying loon	38	4	101	87	7
Night chorusing	15	17	272	430	?
Nest disturbances	9	–	no recordings	–	–
Other animals	2	–	no recordings	–	–

size of the bird. Most of the females were smaller than their mates, but TP ♂ and ♀ were nearly the same size, as were 2RE ♂ and ♀.

BEHAVIOR ASSOCIATED WITH THE TREMOLO

The tremolo can be considered as a distress call for it is generally given in situations that are alarming to the bird (Olson and Marshall 1952, Sjölander and Ågren 1972). Table 2 lists the contexts in which the tremolo was given. In most of these cases the response behavior of the calling bird during or following the call, or a series of calls, indicated a tendency to flee.

Loons have several escape responses. A dive and an underwater swim away from the disturbance is most common, but a bird may also swim or run on the water's surface as a means of escape. The run (described by Olson and Marshall 1952, Sjölander and Ågren 1972, etc.), is similar to the long labored take-off that precedes flight. Flight itself is occasionally used as an escape, but this is quite rare.

I invariably saw one or several of these responses when the tremolo was given by an intruder in a territorial dispute with a resident, or when an unmated individual or a pair without young encountered an approaching boat, low flying or landing seaplane, people or other disturbing stimuli on shore.

The tremolo, however, is often given in situations where avoidance conflicts with a tendency to approach a disturbance. This is most apparent when the call is given during the distraction behavior that occurs when a nest is disturbed, or a chick is threatened by an approaching boat. When a loon moves towards a boat, apparently attempting to draw attention away from its young, its approach is hesitant; it frequently pauses and "spins" or

turns away from the disturbance while calling. Sleeking and lowering in the water (postures that precede a dive), and rapid bill-dipping also occur commonly. These behaviors, as well as quick shallow dives, also occur when the call is given during the water treading distraction display (Munro 1945) that follows a sudden nest disturbance. Bill-dipping in these contexts is part of a larger group of displays referred to as the bill-dipping ceremony by Rummel and Goetzinger (1975). Bill-dipping itself, however, also occurs in other contexts and is generally considered a displacement behavior given in response to disturbing stimuli (Sjölander and Ågren 1972), or in approach avoidance conflict situations (Rummel and Goetzinger 1975).

The tremolo may also be associated with conflict when it is given by an aggressor during the run following a rush at another bird. There is generally little overt aggression during flock displays involving the bill-dipping ceremony (Rummel and Goetzinger 1975), but occasionally a bird will rear up and make a short rush in the direction of another bird in the group. One or both individuals are then likely to begin running while giving the tremolo. If both birds run, the aggressor generally follows the rushed bird. A rush followed by running also occurs occasionally when a resident confronts an intruder within its territory. During such encounters both individuals are likely to give a tremolo. The aggressor, however, never seems to give the call before or during the initial rush, as might be expected if the call communicated a threat or a tendency to attack. Rummel and Goetzinger (1975) found that another call, the yodel, with its associated crouch posture functions as a specialized threat display. My observations agree. Of the nine aggressive rushes in flock displays for which I have complete data, two were preceded by the crouch

TABLE 3. Contexts in which the tremolo was given during flight.

Context	Number of times observed	Tremolo given
Non-resident		
Flies over—resident present	24	22
Flies over—no bird present	9	1
Lands in territory out of view of resident	4	0
Lands in territory in view of resident	2	0
Lands to join flock	12	1
Resident		
Lands to join mate	2	0
Lands alone	2	0
Break-up of flock		
Running precedes flight	6	6
No running before flight	22	7
Territorial		
Intruder takes flight after rush by resident	1	1

and yodel, and the display was also given before each of the territorial incidents. I never saw actual fights so they are apparently rare, but Rummel and Goetzinger described a fight that followed a rush at an intruder in which the crouch and yodel preceded the rush.

I heard the tremolo only during the run that followed the aggressive rush. The run itself appears to be ritualized. I never saw the aggressor overtake the bird it was following (one case was reported by Olson and Marshall [1952], unfortunately they did not mention the vocalizations, if any). The run generally follows a circular path, and as Olson and Marshall pointed out, the following bird never attempt to leave the course taken by the lead bird to cut it off. It is also common for both birds to stop, bill-dip, and then begin running again, all the while maintaining a distance from each other. My data on the timing and relative numbers of calls given by each bird during the run indicate that the rushed bird is more likely to give the tremolo, and that when both birds call, the rushed bird calls first and more often than the aggressor.

The tremolo, when given during the run, probably has a function that is consistent with its use in other contexts; it communicates a tendency to flee. When the call is given by the pursuing bird, it appears to reflect the flight component of an ambivalent aggressive motivation. This may explain my one observation of the aggressor calling as it ran in a different direction from the bird it had just rushed.

When the tremolo is given in the air, its function is not entirely clear, although it often appears to be given as a response to the presence of a territorial resident, perhaps indicating a reluctance to land (see Table 3). In many of the instances in which it was given after take-off, I think that the bird was avoiding aggressive interactions with other birds; either low level aggression in flock displays, or in one case, a territorial encounter with a resident.

CALL TYPES AND BEHAVIOR

Tremolos are normally given in a series in which one or all of the call types may be given, separated by varying pauses. Table 2 gives the distribution of call types associated with each context. It appears, at least for the contexts for which I have data, that all three types can be given in any situation. The only exception is "resident chase intruder" in which I have recorded no type 1 calls. In this case, however, only one chase incident is represented (and only the intruder gave the tremolo), and as is true for most of the recordings, the tape recorder was turned on after the calling began, resulting in the loss of a number of calls at the beginning of the series. The absence of type 1 calls in this context may be a result of either the small sample size or calls missed at the beginning of the one series that was recorded.

Examining the relative distribution of call types in different contexts reveals that type 1 calls were given much less frequently than the other two types, even when the loss of beginning calls is taken into consideration. In most contexts, type 1 calls accounted for 2–9% of the tremolos recorded; although somewhat more for "boats" (15%). In all contexts except "night chorusing," the type 2 call was the most likely to be given, and represented between 50 and 70% of the recordings. During chorusing, the type 3 call was heard most frequently (60% of the time), but in all other contexts, it accounted for approximately 30 to 45% of the calls.

Because of the loss of calls at the beginning of most of the recordings, and the potential for variations in the intensity of the stimuli within each context, Table 2 provides relatively little insight into the effect of different stimuli on the variations in the use of each call type. In Figure 5, however, segments of recordings from individual birds in various contexts have been plotted so as to illustrate the change in pitch frequency of the tremolo as the series of calls progresses. It should be remembered that as the frequency of a par-

ticular call type increases, the length (number of modulations or fractions of modulations) of the frequency level associated with that call type also increases.

Curves 1 and 2 in Figure 5 were recorded from the pair at the east end of Second Roach Pond. Curve 1 represents 2RE ♀ and although the sex of the bird represented in Curve 2 was not certain it also was probably the female. In both cases, the bird was alone with a chick near the center of the territory in a spot where one or both of the adults commonly rested with the chick. The recordings were made as a boat with a small outboard motor passed about 200 m in front of the birds. The calls in Curve 1 were given on 11 July 1976, six days after the chick hatched, and the calls in Curve 2 were recorded two months later on 10 September 1976. The higher frequency calls in the earlier recording may reflect the tension that is apparent in all the loons' activities during the week or two before and after a chick is hatched. By the time the second recording was made, the chick, although not yet fledged, had learned to dive quite well and had become relatively independent. In fact, as the boat approached, the chick dove (after the first type 2 call given by the parent) and was not seen again until well after the boat passed. The parent also dove 10 calls later following a relatively high type 2 call. In the earlier incident, the parent did not dive but remained close to the chick while the boat passed. It gave 15 more type 2 and 3 calls following the last call plotted (a type 2 call), and the series ended without a return to type 1. Both of these series were recorded from the beginning, so the first calls plotted were the first that were given.

Curve number 3 is a series of type 2 and 3 calls recorded from one member of 4RP (the sex was not certain) as a canoe entered the lake about a kilometer away. The recordings were made after the mating season (29 August 1976). Although the canoe was quiet, far from the bird, and no chicks were present, high frequency type 2 and 3 calls were given. This may be because Fourth Roach is the most remote pond in the study area, and is virtually impossible to approach without seriously disturbing the resident loons. Following the ninth type 3 call the bird dove, and its mate, who was farther from the boat, began a series of type 2 and type 3 calls which ended as both birds swam out of view.

Another boat disturbance is represented in Curve 4, recorded in September 1976. In this case, the calls that are plotted were the last 13 of a series of about 27 given by TP ♂ as a
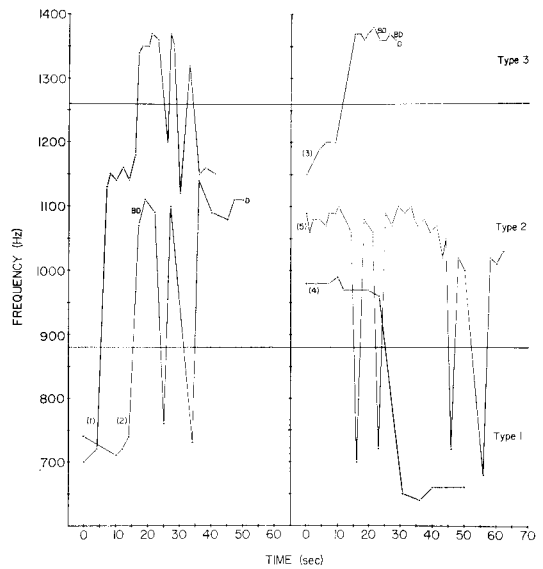

FIGURE 5. Frequency changes in a series of calls from five individuals. D = dive; BD = bill-dip.

small boat (motorless) moved from shore to about 100 m out, and then remained stationary. The bird was alone approximately 300 m away when it first saw the boat and began calling. The calls that preceded the 13 that are plotted were all type 2, and the first 11 or 12 of these were given as the bird remained in one place. The rest of the calls occurred as the bird swam away from the boat, and the type 1 calls at the end of the series were the last that were given. The calls in this series appear to represent a gradual habituation to a constant stimulus.

I have two plots of loons running during a group display involving the bill-dipping ceremony. In the first of these (Curve 5) the calls were given by an individual who ran after displaying with two other birds in a bay in the northeast section of Trout Pond. Their identities are not certain, but TPP were probably involved as well as an unmated individual seen frequently in that area. After a few minutes of displaying, one of the three rushed toward another bird who then ran from the group giving type 1 and 2 calls. Neither the aggressor nor the third bird ran or called. The bird who was rushed ran in a series of sprints interrupted by slight pauses, and it was during these interruptions that the type 1 calls were given. The run continued through 12 more type 2 calls (not shown) and ended just after a type 2 at 1110 Hz. The bird then dove.

The other running incident occurred during a display involving four birds on Second Roach; as in the Trout Pond display, the run-
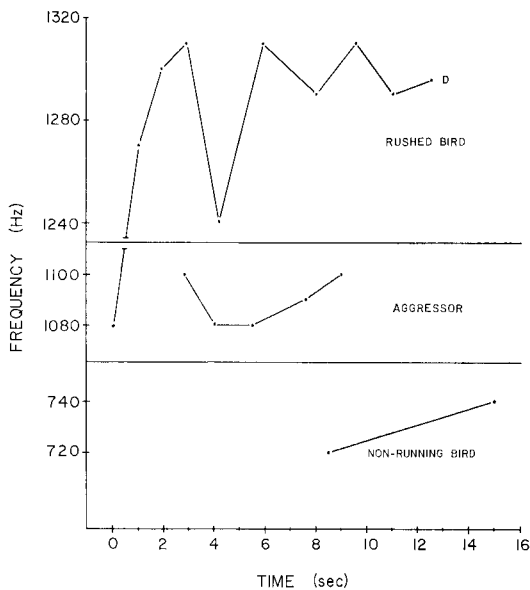
FIGURE 6. Frequency changes as a series of calls progresses. The frequency range between call types has been compressed. D = dive.

ning began after an aggressive rush. In this case, however, the aggressor followed the rushed bird and both of them, as well as one of the non-running birds, gave the tremolo. These calls have been plotted separately (Fig. 6) with the frequency range between call types compressed to better illustrate the relationship between the three birds. The rushed bird began running 2–3 s before the first call was given (two beginning calls were not recorded) and ran without pause until just after the last call. It then dove about three seconds later. The aggressor started its run at about the same time as the other individual, but did not begin calling until after the third call recorded from the rushed bird. I do not know when the aggressor stopped running, but it was probably within one or two seconds of its last call. I did not see the third bird during and immediately after calling but I know that it did not run. Figure 6 shows that the rushed bird began calling first and gave more calls and a higher frequency call type (type 3) than the other two birds. It may also be significant that the individual who did not run gave the lowest frequency call type (type 1). I have few data to compare with this recording because of the difficulties in matching calls with individual birds once running begins, but in the one other case where I could distinguish the calls, the aggressor ran and gave five type 2 calls while the bird it was following gave 27 type 2 calls followed by 13 of type 3. No calls were given by a third bird who was present.

Several generalizations can be drawn from the data in Figures 5 and 6 and from similar measurements made from spectrograms that have not been plotted: (a) a type 1 call never precedes or follows a type 3; (b) pitch frequency generally increases in the calls that precede a change to a higher call type, and the reverse is also true, i.e., the frequency drops in the calls that precede a drop to a lower call type; (c) dives and bill-dips usually follow a relatively high frequency call, although I have too few data to be sure if this effect is generally true.

Figures 5 and 6 also show the relationship between the call type given and the interval between the calls. I found that the mean duration of the interval between two consecutive calls of the same type depends on the call type being given: the pause between two type 2 calls is significantly shorter than than between type 1 calls and longer than that for type 3. Intervals measured from calls chosen randomly from the sample of all calls recorded are as follows (means are in seconds): type 1 $\bar{x} = 3.34$ (n = 16); type 2 $\bar{x} = 2.24$ (n = 68); type 3 $\bar{x} = 0.98$ (n = 49, F = 36.40, df = 2, 129, P < .05).

DISCUSSION

The tremolo call is varied in a regular manner to form three different call types. Each of the variations occurs in every context in which the call is given, and seems to be correlated with changes in stimulus intensity. The call types and their variations may therefore be considered graded forms of the same signal.

As Marler (1967) pointed out, the extensive use of signal grading is unusual in animals. This may in part be accounted for by the difficulties inherent in maintaining signal clarity while introducing graded variations (Konishi 1963). Mistakes would be most likely to occur in cases where a number of morphologically similar signals code qualitatively different (discrete) messages. In vocal communication, this problem may be overcome by grading the amplitude, or varying the interval between the signals. Such simple forms of grading, which leave the structural characteristics of the sound unaltered have been reported in a number of birds and mammals (Jay 1965, Chamberlain and Cornwell 1971). If, however, a structural variation is used for grading, one would expect other properties of the sound to remain unaltered (Konishi 1963). For example, the multiple

rack alerting call of the Piñon Jay (*Gymnorhinus cyanocephalus*), which is similar in structure to the rack contact call, is graded by varying the number of notes in the call, but the harmonic structure, duration, and interval between the notes remain relatively unchanged (Berger and Ligon 1977).

The accuracy of communication of graded signals would be increased if information were available to other senses. Consequently, one would expect grading to occur in close range communication by diurnal species living in close-knit social groups (Marler 1967). These conditions are satisfied in most of the species for which grading has been reported. The loon, however, maintains a large territory throughout the breeding season and as a result often communicates out of sight over long distances. Furthermore, graded vocalizations are frequently given at night. Signal clarity is maintained under these conditions by the limited number of discrete vocalizations used by loons. Besides the tremolo, there are only three relatively simple calls, each of which has a distinctive structure. The wail has three variations given in approximately the same frequency ranges as the tremolo, but the notes which make up the call are unmodulated. The yodel is a combination of modulated and unmodulated tones with a longer duration and wider frequency range than the other calls; and the hoot is a single modulation given in the frequency range of the type 1 tremolo. These differences among calls permit considerable latitude for varying the structural characteristics without obscuring their distinctiveness.

All the loon vocalizations show elements of grading, but the variations of the tremolo are the most elaborate, and provide a potential for reflecting a wide range of differences in motivation. The type 1 is associated with low levels of stimulus intensity, but can itself be graded by increasing the number of modulations and their frequency. Type 2 and 3 calls correspond to further increases in intensity, and are formed by adding new harmonically unrelated frequency components. Again, as with the type 1 call, types 2 and 3 can be graded by increasing the duration and frequency of their respective frequency levels. The three call types evidently correspond to coarse adjustments to stimulus intensity, and the variations within types to more subtle refinements.

Variations in frequency both within and among call types are apparently the key feature in coding the signal. However, individual differences in fundamental frequency are occasionally greater than the frequency range between two call types (see for example TP♂ and BL♀). This presents a problem in signal recognition similar to that encountered in discrete versus graded coding, and species-individual distinctions. It has apparently been resolved by retaining one or more introductory modulations in level 1 of the type 2 and 3 calls. This provides a frequency reference to distinguish each of the call types regardless of the frequency variations among individuals. Further definition of the call types may be provided by the frequent occurrence of a concluding modulation in type 2 and type 3 calls, and the occasional return of a modulation to level 2 of the type 3 call. Brooks and Falls (1975) have suggested a similar form of pitch discrimination as a means of individual recognition in the White-throated Sparrow (*Zonotrichia albicollis*). Pitch changes in human tone languages (Burmese, Chinese, etc.) occur with reference to preceding words and syllables (Franklin and Rodman 1974).

Whatever ambiguity may remain is overcome by the redundancy of the grading. The tremolo is modulated in amplitude as well as in frequency, and a preliminary examination of oscillograms indicates that amplitude varies with frequency; a type 2 call is louder than a type 1, and a long type 2 is louder than a short one. Because of the significant variations in amplitude that result from slight changes in head position, this property alone is not likely to provide a clear signal, but it may add definition when used in conjunction with other variables. Finally, the interval between the calls is changed depending on the call type being given. Thus, there are four variables that when used together accurately reflect the motivational range of the message: frequency, duration, amplitude and call interval.

Some features of the tremolo are less variable. The modulation rate and range remain relatively constant, providing a framework around which the other variables are introduced. This allows a further means of maintaining the discreteness of the tremolo, but it may also provide information regarding species identification. The tremolo of the Yellow-billed Loon has a considerably slower rate of modulation (Sjölander and Ågren 1976) indicating, perhaps, that this feature of the call is a species-specific characteristic.

With the possible exception of the differences in fundamental frequency, there are no clearly identifiable individual characteristics

of the tremolo. Certain features of the yodel call, however, may serve this function (Rummel and Goetzinger 1975).

With the extensive use of grading in loon communication, one would expect graded signals to elicit graded responses. The chasing behavior in loons may provide opportunities for studying this relationship. The calls of the chased bird should reflect its perception of the motivation of the aggressor. This may in part be determined by the calls given by the aggressor: higher frequency call types indicate a greater reluctance to attack. One might therefore expect an inverse relationship between the call types of the two birds. In the recordings in which I could distinguish the vocalizations of each bird, the individual being pursued did, in fact, give higher frequency call types than the aggressor. However, further study will be needed to determine if the variations in an aggressor's calls are correlated with the calls and behavior of the bird it is pursuing.

SUMMARY

The tremolo is an alarm call generally associated with some behavioral indication of a tendency to flee. It is also given in approach-avoidance conflict situations. Data from field recordings indicate that there are three distinct structural variations (call types), which are formed by the addition of progressively higher harmonically unrelated frequency components. The pitch frequency of each of the call types varies depending on its duration: the longer the call, the higher its frequency. The amplitude and the interval between calls are correlated with the type given. Each of the call types and their variations occur in every context in which the call was recorded, and appear to be correlated with changes in stimulus intensity. They are therefore considered graded forms of the same signal.

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