

Vocal repertoire, harmonic structure, and behavioural context in Red-throated Loon (*Gavia stellata*)

SHEILA D. DOUGLAS¹ and THOMAS E. REIMCHEN^{2,*}

¹112 Olive Street, Victoria, British Columbia V8S 3H3 Canada

²Department of Biology, University of Victoria, P.O. Box 1700, Victoria, British Columbia V8W 2Y2 Canada

*Corresponding author: reimchen@uvic.ca

Douglas, S.D., and T.E. Reimchen. 2021. Vocal repertoire, harmonic structure, and behavioural context in Red-throated Loon (*Gavia stellata*). Canadian Field-Naturalist 135(2): 165–180. <https://doi.org/10.22621/cfn.v135i2.2569>

Abstract

Among the five loon species (Gaviidae), Red-throated Loon (*Gavia stellata*) is the oldest lineage and is the most divergent in morphology and vocalizations. We substantially expand earlier description of calls for a nesting pair and non-breeding birds on Haida Gwaii, British Columbia, Canada. Three major calls used by the nesting pair (Quack, Wail, Plesiosaur) were all low frequency (700–3000 Hz) with multiple harmonics, calls that were also used by non-breeding birds without territories that overnight on freshwater lakes. Call duetting in the Wail and Plesiosaur, as well as sexually dimorphic frequencies and structure within the duets, typically occur in territorial display or pair interactions. The nesting pair used several calls audible only at short distances (Coo, Extended Coo, Staccato, Soft Raack) that were low frequency (200–1200 Hz), graded in behavioural intensity and that resulted in chick responses, including feeding or return to nest. A high amplitude Loud Raack was used by the female and is associated with flight incentives for pre-fledged chicks. Vocalizations of chicks, usually feeding solicitations to the adults, develop from simple chirps in the first week following hatch to more complex calls resembling the Wail and the Plesiosaur calls just prior to fledging. Although the majority of our acoustical descriptions are limited to a single nesting pair where sexes could be differentiated, these represent the first quantification of sound frequency, harmonic structure, and duration, most often associated with context-specific responses, and are suggestive of syntactical content to the vocal repertoire of this basal taxon.

Key words: Avian song; duetting; Drizzle Lake Ecological Reserve; *Gavia stellata*; Gaviidae; Haida Gwaii; harmonic structure; sexual dimorphism; sonogram; vocalizations

Introduction

The widely recognizable vocalizations of loons (Gaviidae) commonly define the acoustic landscape of northern hemisphere lakes and, as with many avian species, calls have multiple functions (Catchpole 1982; Wiley and Richards 1982). In addition to territoriality, studies in Common Loon (*Gavia immer*), the most southerly of the loon species, demonstrate that their vocalizations also include information such as levels of aggression (Rummel and Goetzinger 1975; Mager and Walcott 2014), body condition (Mager *et al.* 2010), competitive ability (Walcott *et al.* 2006), and possibly individual recognition (Walcott *et al.* 1999, 2006; Mager *et al.* 2010). Such characteristics support emerging views in animal communication that intraspecific variation in call structure can have referential or syntactical context (Templeton 2005; Wilson and Evans 2012; Suzuki 2016).

Red-throated Loon (*Gavia stellata*) is the most northerly of the loons; they are ecologically distinct

in nesting on ponds or small lakes, often without fish, and flying to larger water bodies to capture and return fish to the territory (Huxley 1923; Reimchen and Douglas 1984a). This species appears to be the least derived morphologically from fossil loons and is considered the sister group to all other Gaviidae, possibly with a 20 million year separation time from other loons (Sprengelmeyer 2014). Consequently, the vocalizations of this basal taxon are of considerable interest for comparative analyses. Early investigations were descriptive (Selous 1912; van Oordt and Huxley 1922; Huxley 1923; Johnson and Johnson 1935; Keith 1937). Sjölander (1977), provided the first sonogram sketches and situational information for vocalizations and visual displays, and offered a framework for comparisons among loon species (Sjölander 1972, 1976, 1978). We provided audio tapes, basic call descriptions, and information on behaviour associated with several calls of Red-throated Loon on Haida Gwaii, British Columbia as personal

communications which were then included in summaries of Red-throated Loon life history (Barr *et al.* 2000; Rizzolo *et al.* 2020). In the current manuscript, we present additional data on vocal repertoire, acoustic structure of calls, and behavioural contexts of vocalizations of a breeding pair of Red-throated Loons on an ecological reserve during the nesting period, as well as vocalizations of non-breeding birds that occupied the reserve nocturnally during the summer (Reimchen and Douglas 1980). Because the sexes exhibit differences in behaviour in feeding the young, in territorial defense, and in responses to territorial intrusions (Reimchen and Douglas 1985), we give special attention to differences between the sexes in calls. We document duetting behaviour of nesting pairs and examine some of the ontogenetic changes in vocal structure.

Methods

During biophysical surveys of 184 ponds and lakes on Haida Gwaii, British Columbia, Canada (1976–1989), we located 34 nesting territories of Red-throated Loons (Douglas and Reimchen 1988a). While the vocal behaviour was generally comparable among breeding pairs throughout this area, the diversity and specificity of calls encouraged closer study. Consequently, on an ecological reserve in the same archipelago, we collected observational, video, and audio data on nesting and non-breeding Red-throated Loons, which allowed us to broaden their described repertoire, characterize the contexts of calls and the extent of sexual dimorphism, and document the ontogeny of vocalizations. Simultaneous studies on the parental contribution to feeding regime throughout the seven-week pre-fledging period (Reimchen and Douglas 1984a) and on differential roles of the sexes in feeding and territorial defence (Reimchen and Douglas 1985) allowed a broad ecological context to the structure and function of calls.

Drizzle Lake Ecological Reserve is located on a broad expanse of *Sphagnum* bog, ponds, and lakes on the north-eastern region of Haida Gwaii, British Columbia (53.934056°N, 132.072184°W). Thirty-six species of aquatic birds have been observed on this 110 ha dystrophic lake, the majority showing regular seasonal and numerical abundance, of which Red-throated Loon and Common Loon accounted for the greatest yearly numbers (Reimchen and Douglas 1984b). Non-breeding Red-throated Loon, usually in pairs, occupied the lake from April to August, generally flying in from adjacent marine waters at dusk and leaving at dawn, with maximum evening numbers (19) occurring in July (Reimchen and Douglas 1980, 2021). Common Loons, none of which nest on this lake, were daily visitors, primarily diurnal, with peak

numbers (83) in July (Reimchen and Douglas 1980, 2021). Nesting Red-throated Loons laid 14 clutches in the watershed (1976–1986; Douglas and Reimchen 1988b, 2021).

Non-breeding Red-throated Loons were observed from an elevated platform on the lake shore while breeding birds were observed from blinds within 8 m of the nests. General observations of abundance and distribution of non-breeding loons were maintained during 1977–1985 (Reimchen and Douglas 1980, 1984b). Three types of data were used for analysis: written observations, audio recordings, and video recordings.

Written observations

A total of 3620 written observational records consisted of (a) 2913 records of the breeding pair and pre-fledged young at Drizzle Lake (27 July–14 September 1982, 348.5 h), (b) 606 records of non-breeding birds (4 April–13 September 1980, 101.6 h; 14 April–14 May 1983, 21.3 h), and (c) 101 records of the pair with young on the bog pool (1 August–8 August 1981, 22.7 h). Each record contained date, time, location, identity (species), chick age, sex (when possible), breeding or non-breeding, type of vocalization or visual display and its context, the behaviour of other species that the birds interacted with and, for breeding birds, behaviour related to feeding or to infringements into the territory (~50 m radius from the shoreline nest) by other species. In written records, calls of breeding adults to pre-fledged young were grouped as “low calls”, although later analysis with audio and video showed four distinct calls.

Audio recordings

Audio recordings were made in 1984 to quantify call structure. Vocalizations of a single pair of breeding Red-throated Loon and their two chicks and several non-breeding birds on Drizzle Lake were recorded using a Uher 4000 Report Monitor Tape Recorder (München, Germany) and a Dan Gibson parabolic microphone (EPM 200). Recordings were made on 24 days from 11 June to 2 August, for a total of 217 min covering 118 vocal bouts (89 bouts of the breeding pair and their two chicks, 29 of non-breeding, and six of both groups together). Playback of audio recordings was measured for duration of bouts, and in some cases, call durations and call interval lengths. Sonograms of recorded calls were made on a Kay Elemetrics Digital Sonagraph 7800 Analyzer and 7900 Printer (Lincoln Park, New Jersey, USA). Several calls from different bouts for each call were analyzed over the 8000 Hz range at both 45 Hz (for frequency discrimination) and 150 Hz (for time discrimination) bandwidth filters. For comparison of successive calls, a frequency range of 4000 Hz was used to extend the

sonogram to 5.12 s duration. Frequency and duration data were obtained from sonograms using grids marked in Hertz (Hz) or in mm (converted to ms). The margin of error is ± 60 Hz and ± 0.008 s. The term “amplitude” is used in a relative sense because amplitude was not quantified on sonograms.

Video recordings

Video recording using a Sony Portable Videorecorder (AV-3400, Japan) equipped with an f 12.5–75 mm zoom lens or 1000 mm fixed lens were made of non-breeding loons in 1981 and two breeding pairs in 1980–1984, including recordings of two chicks in 1984 (1050 min). For breeding birds, recordings were primarily made of feeding of young by adults; in most feeding bouts, vocalizations were recorded with the videorecorder microphone. Video recordings of visual displays were analyzed to produce descriptions of displays and to link vocal and visual displays. Contexts of different low amplitude calls were obtained from video recordings. Because sex of the adult birds was known for each recorded feeding bout, verification of sexual dimorphism in calls was possible.

Representative audio recordings were uploaded to the Macaulay Library at the Cornell Lab of Ornithology (see Appendix 1 for accession numbers and hyperlinks). Quantitative data of vocalizations (duration, intervals, sound frequencies) were compared with unpaired *t*-tests and analysis of variance (ANOVA; SPSS v25, IBM, USA).

Results

Vocalizations of nesting and non-breeding adult Red-throated Loon had dominant frequencies from 700 to 3000 Hz and all showed harmonics in at least one segment of the call. Although the different calls shared characteristics and sometimes were continu-

ous, we recognized nine calls based on their acoustic characteristics, five of which were higher amplitude (Quack, Wail, Plesiosaur, Kark, Loud Raack) and four lower amplitude calls (Coo, Extended Coo, Staccato, Soft Raack) that were used in adult-chick interactions.

Quack

Context—The Quack was used almost exclusively in flight (99.3%, $n = 292$ bouts comprised of about a dozen birds every night throughout the breeding season) by nesting and non-breeding adult Red-throated Loons of both sexes during lake arrivals, departures, and over-flights. This call was also heard in flight over marine waters. Conspecifics on the surface responded to the in-flight Quack with surface vocalizations and displays (Wail, Plesiosaur).

Acoustic structure—The basic Quack is a single syllable call averaging 99 ms (range 72–112, SE 2.9) in duration ($n = 19$) between 1000 and 2000 Hz with approximately two or three dominant harmonics within each call, repeated about three to four times per second (Figure 1, Appendix 1). Quacks occurred in all birds and were given repeatedly in flight; we quantified this call in the nesting pair. The calling rate increased towards the end of each bout as the birds approached the lake but they did not Quack as they descended to the surface. Average intervals between Quacks (149 ms) varied within and among bouts (range 106–277, SE 8.3, $n = 33$ intervals in four call bouts from the breeding pair). During the final approach to the lake, the loons often (proportions not recorded but heard many times over many years) gave a distinctive extended Quack, approximately three times the duration of a single Quack, ending in a short (~100 ms) ‘note’ of a single dominant harmonic rising and falling near 1700 Hz.

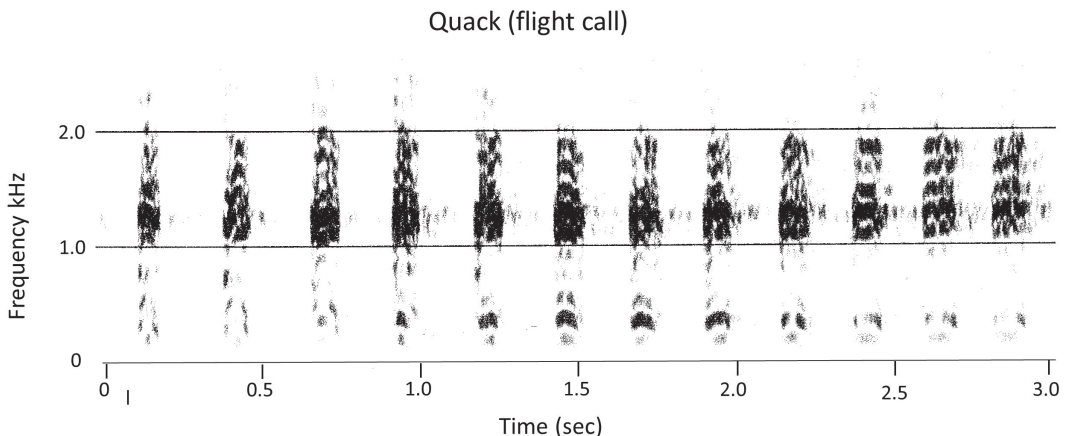


FIGURE 1. Representative Quack sequence of the dominant (99%) flight call given by Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. Bandwidth filter: 150 Hz.

Kark

Context—This is a warning call and made primarily on water (78%, $n = 83$, other 12% in flight) by nesting Red-throated Loons, either singly or in pairs in response to lake or shoreline intrusions into the territory.

Acoustic structure—The Kark is a single syllable call, averaging 204 ms (range 152–240, SE 7.4, $n = 14$ from the nesting pair) between 1000 and 2000 Hz, similar in structure to the Quack, but audibly distinct in having significantly longer durations (unpaired $t_{31} = 14.1$, $P < 0.001$) and arrhythmic repetition within bouts (Appendix 1). Numbers of harmonics ranged from three to five in 10 different Kark calls. Unlike the Quack, intervals between Karks were highly variable, both within and between bouts, ranging from single to multiple calls. The maximum recorded rate was 23 Karks in 27 s by the nesting pair when a Bald Eagle (*Haliaeetus leucocephalus*) perched on a tree near the nest. In a Kark bout by the male of the nesting pair, intervals between eight calls varied from 1.5 to 8.6 s, with intervals increasing between each successive call. During execution of the call, the neck was vertically extended, with the head held horizontal to the water or angled slightly up.

Wail

Context—The Wail includes a diversity of closely-related calls that are voiced on the lake surface both by nesting pairs, singly or as a duet (cooperative vocalizations by pair-mates), or by non-breeding individuals. The most consistent use was in response to conspecifics in flight that were vocalizing Quacks above the lake. The actual number heard would be in the thousands as this was the most common vocalization on the lake and was heard in response to approaching Red-throated Loons in flight and occurred for every arriving pair throughout the summer each year. Of 113 bouts of Wails in the nesting territory, 53% were performed as duets. Wail duets were in some cases antiphonal (calls of the two birds alternating and non-overlapping). For example, following the flight of a Bald Eagle over the territory the male and female nesting pair performed an antiphonal Wail bout lasting 245 s, in which the female wailed 32 times and the male 37 times. As well, the pair had duets of overlapping wails (e.g., in a 54 s bout, the female made three calls while the male made nine calls; in a 120 s bout, the female made 42 calls while the male made 22 calls). Nesting pairs also used the call on detection of potential threats including overflight of Bald Eagles and Common Raven (*Corvus corax*) near nesting territories. Loons displayed a distinctive posture during the Wail (Figure 2 inset drawing). From a head up position, the head and neck move forward and down. By the middle of the call, the head and bill are

parallel to the water and the lower part of the neck is immersed; the bird remains in that posture until the end of the call. When the neck is outstretched, the throat directly below the rictus is distended. During parental feeding, the fish held in the adult's bill did not appear to alter the posture or sound characteristics of the Wail. This call was never observed with the neck and head in a normal upright position.

Acoustic structure—The Wail, ~1 s in duration (details below), has two dominant harmonics near 1000 Hz and 2000 Hz, initial frequencies rising ~300 Hz in the first quarter of the call and gradually decreasing towards the end (Figure 2, Appendix 1). The female of the nesting pair (Figure 2a) produced Wails that are ~150 Hz higher frequency than the male (Figure 2b) during the central (average 1100 versus 965 Hz, unpaired $t_{17} = 2.51$, $P < 0.02$) and terminal phase (average 880 versus 720 Hz, unpaired $t_{16} = 2.43$, $P < 0.05$) of the call and marginally, but not statistically higher, during the onset (average 960 versus 800 Hz, unpaired $t_{17} = 1.46$, $P < 0.25$). The beginning of the call had the highest variability in number of harmonics (2–8 for the female and 2–13 for the male). The female occasionally had a “croaking” quality evident as an ~1000 Hz band of noise around the dominant harmonic. Duration of the individual Wails was marginally, but not significantly, longer in the female (average 1266 ms, range 1161–1663, SE 56.7, $n = 9$; male 1158 ms, range 714–1471, SE 66.4, $n = 10$; unpaired $t_{17} = 1.29$, $P = 0.23$). Individual Wails were often given in succession, the length of which varied with the context: several Wails occurring with the over-flight of other Red-throated Loons to continued Wailing when Bald Eagles were present in the territory.

Plesiosaur

Context—The Plesiosaur is a high amplitude call and stereotypic display used by both nesting and non-breeding loons. For nesting birds it was performed, individually or in duet, when the partner arrived in the territory or prepared to depart; a Plesiosaur bout was often a progression from a Wail duet elicited by in-flight Quacking of a loon over the territory (Appendix 1). We heard this often (not quantified but less than frequent and more than occasional) when watching nesting pairs on multiple years. It was also used during territorial intrusions from Common Loons and conspecifics. In the latter case, intruders occasionally (not quantified) participated in the Plesiosaur calling. Non-nesting birds in the centre of the lake commonly performed the Plesiosaur call and display, individually or in groups, usually directly following a Wailing bout in response to conspecific overflights. We were not always able to determine the stimulus for Plesiosaur calls in these loons because they occupied the lake in low light conditions during twilight.

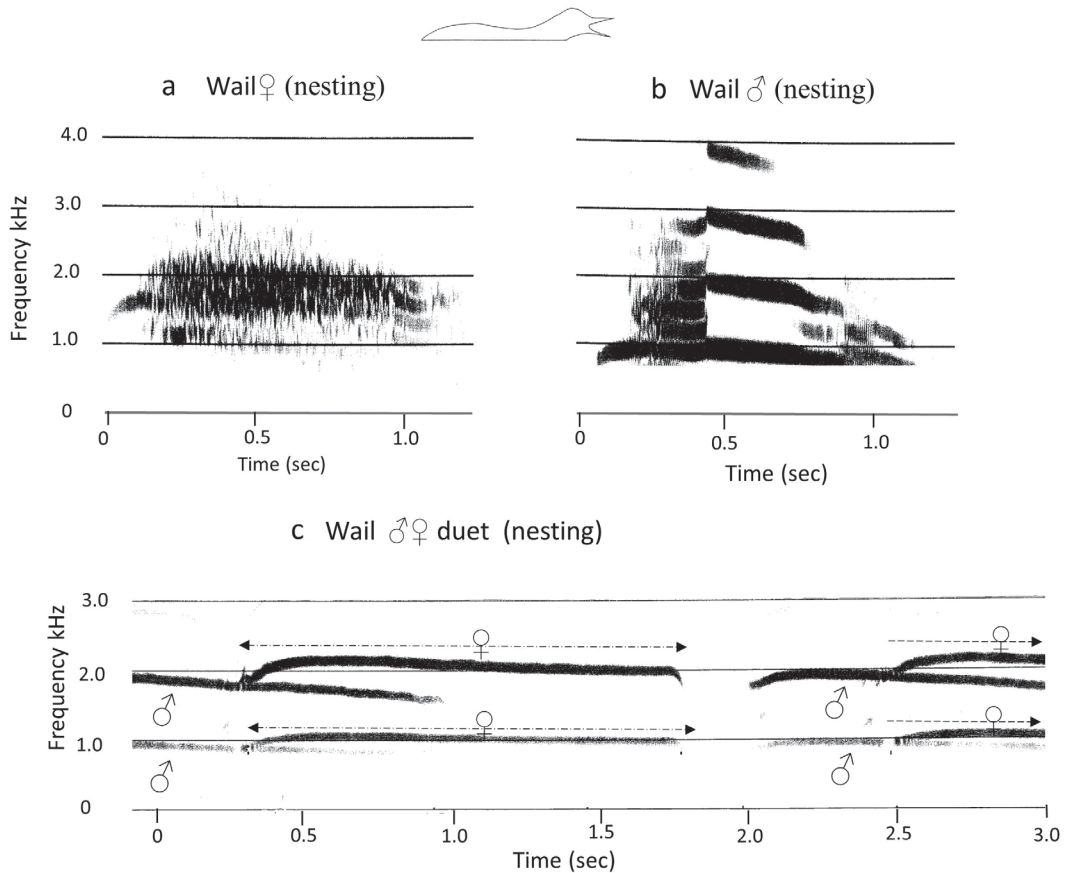


FIGURE 2. Variation in Wail calls given by a nesting pair of Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. a. female, b. male, c. female/male duet. Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

Acoustic structure—The Plesiosaur is a structurally complex sexually dimorphic call (Appendix 1). The female call (Figure 3a) consisted of broadband noise in the range of 1000–2500 Hz that had a growling or rattling quality. Underlying harmonics show a dominant mean frequency near the central part of the call at 1610 Hz (range 1500–1825, SE 46.5, $n = 6$ from the nesting pair) and the call terminated in a short, ascending phrase that lacked a noise overlay (dominant frequency average 1459 Hz, range 1375–1500, SE 56.8, $n = 7$). Durations of the female Plesiosaur call and intervals between calls in a bout were relatively consistent (duration: average 435 ms, range 400–576, SE 9.14, $n = 24$; intervals: average 213 ms, range 160–272, SE 11.2, $n = 11$). The male of the nest pair Plesiosaur call (Figure 3b) had a dominant frequency that ranged from 750 to 1160 Hz (average 963, SE 41.7, $n = 18$) throughout most of the call, with a rapid increase in frequency at the

end of the call (range 950–1500 Hz; average 1123, SE 88.6, $n = 6$). Superimposed on this was a band of rapid sound pulses covering a frequency range of 750–2750 Hz; this made the vocalization appear like rhythmic pulses of noise rather than a structured call. Durations of the call by the nesting male (average 821 ms, range 71–959, SE 15.3, $n = 18$) were about twice as long as those of the female (note that all sonograms did not have complete information hence the different sample sizes from the nesting pair). Plesiosaur calls by a non-breeding bird (Figure 3c) showed comparable structure to that of the nesting male, differing primarily in its frequency range. Individual Plesiosaur calls by non-breeders were difficult to isolate aurally and in sonograms because the recorded birds were usually in groups and at a distance. In the nesting pair, the call and display occurred primarily (81%, $n = 100$) as a duet, in which there were few silent segments (Figure 4). In groups of non-breeding birds that

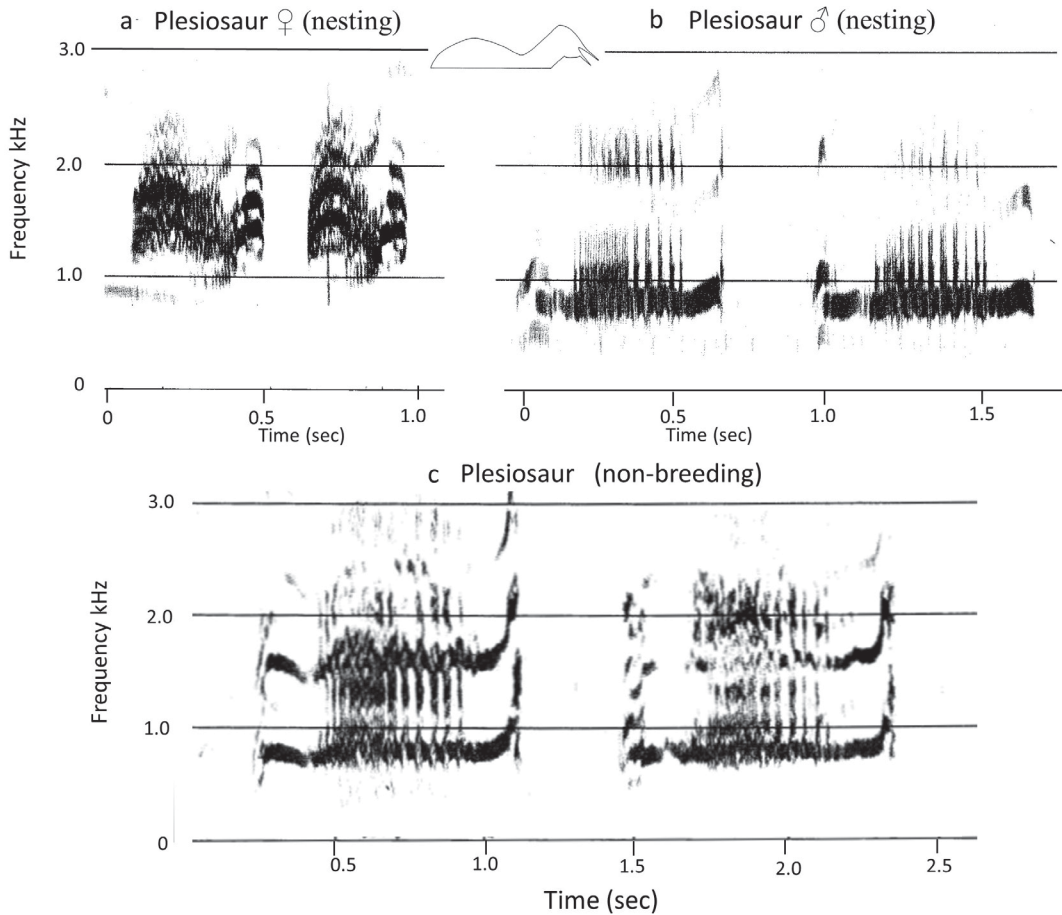


FIGURE 3. Variation in Plesiosaur calls of a nesting pair and non-breeding Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. a. female and b. male of nesting pair. c. Non-breeding adult Red-throated Loon (similar to male call but sex could not be reliably determined). Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

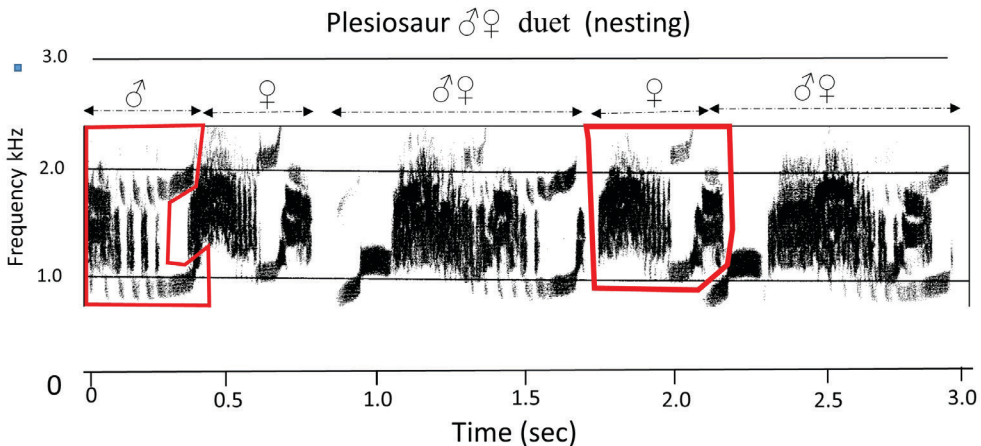


FIGURE 4. Duetting Plesiosaur call of a nesting female/male pair of Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. Separate male and female calls are outlined. Bandwidth filter: 150 Hz.

aggregate on the lake during dusk, up to seven loons were observed participating in a Plesiosaur call and display and in most instances, these bouts were preceded by Wail bouts.

Display—The majority (97%) of Plesiosaur calls ($n = 243$, all from the breeding pair) were accompanied by the Plesiosaur display, the few exceptions occurring during calls in flight (six cases) and on the nest (one case). In the Plesiosaur display (Figure 3 inset drawing), termed the “Plesiosaur race” and “snake ceremony” by Huxley (1923), the body is held high in the water with the neck arched and the head angled downward, with the bill tip at water level or immersed. The neck appears to be contracted in length and greatly expanded in circumference; the throat immediately below the rictus is distended. After a bout or between calls the birds often shake the head and bill. The male of the nesting pair was seen to Plesiosaur call and display with a fish in the bill. A variation on the display is a “winged” Plesiosaur, where one or both of the wings are held out of the water but bent at the wrist and angled slightly backwards so that the wing tip is immersed. The bird alternately extends the left and right wings, changes in wing extension coinciding with changes in direction of movement through the water, or both wings may be extended simultaneously. Most Plesiosaur displays involved abrupt changes in direction and loons sometimes traced a zigzag path through the water.

Vocalizations by the breeding pair associated with parent-chick interactions

Context—Seven calls were used by the adults of the breeding pair to solicit responses from their chicks. Four were low amplitude (Coo, Extended

Coo, Staccato, Soft Raack) and were voiced primarily during feedings. Typically, an adult returned from the ocean with a marine fish in its bill and vocalized to a chick on the nest; in response, a chick entered the water and attempted to grasp and swallow the fish, after which it would be called back to the nest by the other adult. There were also three high amplitude calls used in parent-chick interactions. Two of these, the Wail and the Kark were given during proximity of the Bald Eagle (see Table 1 for number of times), following which the chicks either dove or swam rapidly to the shoreline where they sheltered in the emergent vegetation. A third high amplitude call was the Loud Raack used by the female in flight as a flight incentive to the chick during the week prior to fledging, usually followed by the young swim-flying over the water surface and attempting to take off.

Acoustic structure—The Coo (Figure 5a), only heard and recorded for the male (but heard in all nesting years), is a short (average 82 ms, range 56–96, SE 3.3, $n = 20$) low frequency (200–1200 Hz) call with multiple harmonics that was given singly or in short bouts. Frequencies could increase by 300 Hz during the initial part of the call and there were usually at least four harmonics. The length of Coo bouts varied considerably, as did the call rate within bouts (e.g., 15 Coos in a 90 s bout and 81 Coos in a 143 s bout). Coo bouts were sometimes followed by Extended Coo or Staccato bouts. The Extended Coo (Figure 5b), also only vocalized by the male, had a frequency and harmonic structure similar to the Coo, but longer duration (average 934 ms, range 625–1175, SE 66.3, $n = 10$), and with abrupt changes in dominant frequencies and number of harmonics within the call. During the calls, the adult assumed a normal body

TABLE 1. Calls used by a pair of breeding Red-throated Loon (*Gavia stellata*) during interactions with conspecifics and other bird species on Haida Gwaii, British Columbia, Canada. This includes interactions within the breeding territory and instances in which calls of other birds were audible within the territory. Species with fewer than five interactions excluded. RTLO = Red-throated Loon (*Gavia stellata*); COLO = Common Loon (*Gavia immer*); CORA = Common Raven (*Corvus corax*); BAEA = Bald Eagle (*Haliaeetus leucocephalus*); GWTE = Green-winged Teal (*Anas carolinensis*); CAGO = Canada Goose; BEKI = Belted Kingfisher (*Ceryle alcyon*); RNGR = Red-necked Grebe (*Podiceps grisegena*); GLGU = Glaucous-winged Gull (*Larus glaucescens*); SCAU = scaup (*Aythya* sp). A single interaction between Red-throated Loon and Bald Eagle which might last an hour, could have 50 sequential wails but this is considered one interaction.

Species	RTLO	COLO	CORA	BAEA	GWTE	CAGO	BEKI	RNGR	GLGU	SCAU
Interactions (n)	405	135	129	59	33	24	13	12	8	6
Vocal bouts (n) comprised of the following types of calls:	91	21	32	25	3	1	2	0	1	1
Wail	36	9	24	24	1	1	2	0	0	1
Plesiosaur	31	8	0	0	0	0	0	0	0	0
Kark	16	2	8	1	2	0	0	0	0	0
Loud Raack	6	0	0	0	0	0	0	0	0	0
Low calls*	2	2	0	0	0	0	0	0	1	0

*Coo, Extended Coo, Staccato, Soft Raack.

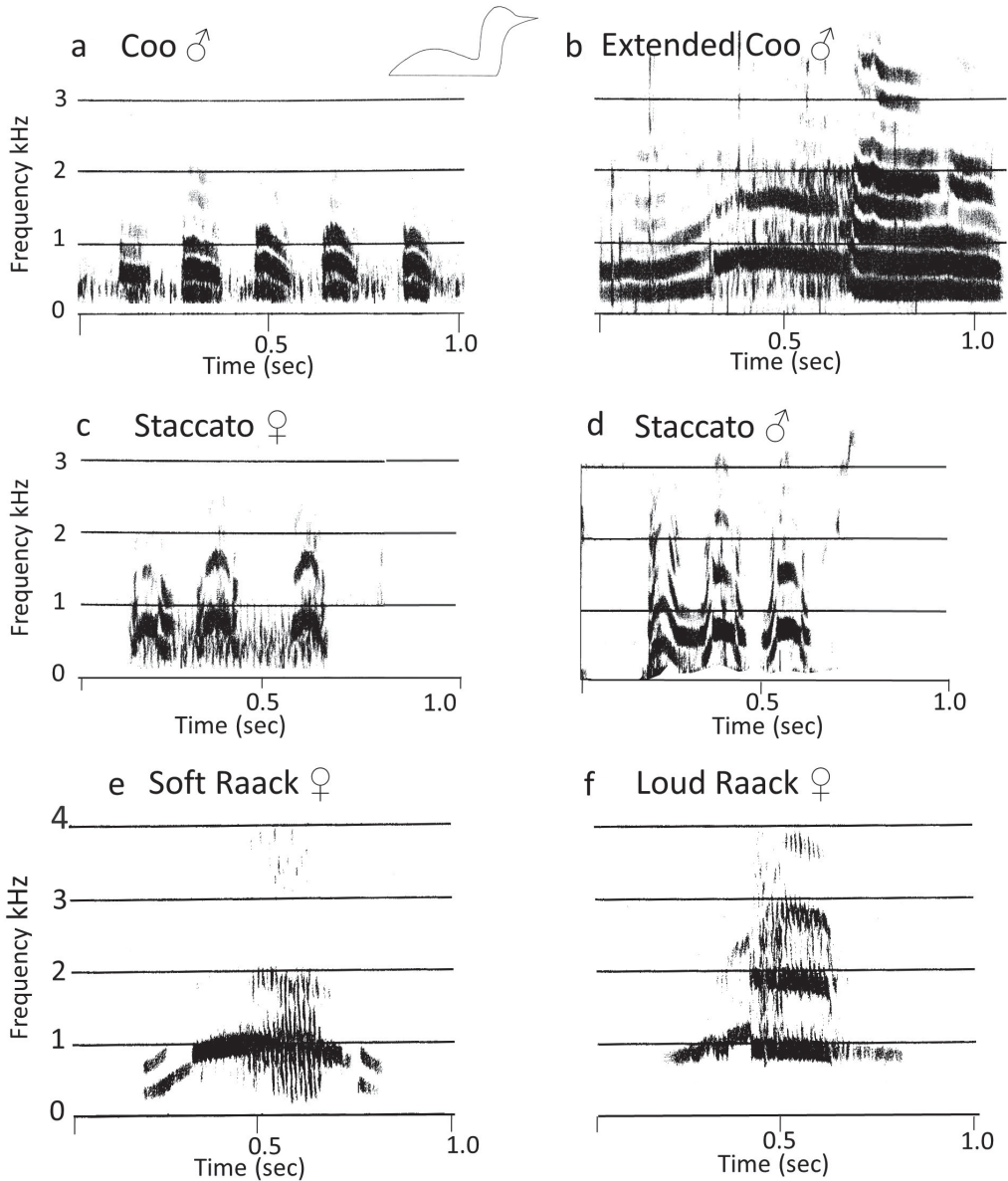


FIGURE 5. Representative vocalizations of a pair of adult Red-throated Loon (*Gavia stellata*) to their pre-fledged chicks in their nesting territory. a. Coo-male. b. Extended Coo-male. c. Staccato-female. d. Staccato-male. e. Soft Raack-female. f. Loud Raack-female. Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

posture with no noticeable changes in bill opening. The Staccato, a short low frequency (500–2000 Hz) call occurring singly or in groups up to five was recorded for both the adult female (Figure 5c) and male (Figure 5d) and was the major (55%) feeding solicitation call. Number of harmonics varied from two to five, with the first harmonic the dominant frequency throughout and in each of the harmonics,

the call had an initial increase in frequency, a central high amplitude phrase, and a terminal decrease in frequency. Dominant frequencies (measured in the central part of the call) were similar for the female (average 732 Hz, range 700–750, SE 11.1, $n = 5$) and male (average 756 Hz, range 680–810, SE 8.1, $n = 19$), respectively, as were the mean duration of calls (female average 90 ms, range 80–96, SE 1.5,

$n = 5$; male average 90 ms, range 56–138, SE 4.6, $n = 24$). Call rates ranged from 0.15/s to 0.73/s with total bouts ranging from 14 to 148 calls. Associated with the Staccato was a sporadic rapid bobbing of the head and bill which increased the conspicuousness of the fish to the chick; the fish was often reoriented in the adult's bill. The adult held its neck at an oblique angle and the fish's tail often dipped in the water. In the majority of cases, chicks responded to the vocalization with feeding behaviour, such as leaving the nest, swimming to the adult bird, or pecking, grasping, or swallowing the fish. The Soft Raack (Figure 5e), recorded only for the female, lasting about 600 ms, is initiated with a fundamental frequency near 325 Hz that increases gradually to a dominant harmonic near 800 Hz at a higher amplitude and ending with a short descending tone back to its initial low frequency. The call has up to three harmonics. The most distinct characteristic of the call was the superimposition of a wide-frequency band of "noise" that overlay the central part of the call, spanning frequencies of about 100–6000 Hz. The Loud Raack (Figure 5f, Appendix 1) was distinctly louder and harsher than the Soft Raack. We were only able to record several of these calls but it had a structure similar to the Soft Raack, with a low frequency onset (average 760 Hz, range 700–800, SE 27.8, $n = 4$), a high amplitude and frequency central phrase (average 900, range 780–970, SE 61.7, $n = 3$) at the beginning and a lower amplitude and frequency ending. The dominant frequency was the fundamental. Loud Raacks were most often given in short series (e.g., five calls in 34 s). Similar to the Soft Raack, the call had an overlay of noise, ranging in frequency from 625 to 4000 Hz. Gradation between the two calls was heard on one occasion, when a Soft Raack was transformed into a Loud Raack by increased amplitude.

Vocalizations of chicks

Chicks of the nesting pair displayed a diversity of calls, ranging from simple chirps near hatching to calls closely resembling those of the territorial adults near fledging. The vocal repertoire (Figure 6) increased over the 46 day pre-fledging period. The simplest call was the Chirp that was used throughout and was associated with begging behaviour. The Chirp is a repeated short duration call with a dominant frequency at 2200 Hz and a second harmonic at 4600 Hz with a slight (100 Hz) ascending and descending variation over the call (Figure 6a). The Chirp, usually repeated 1/s (up to 86 Chirps/73 s) was given on the nest or in the water. By day four and five, the chicks began to vocalize a longer and more complex call that initially ascended and rapidly flipped between a dominant harmonic at 2200 and 3000 Hz in the central part of the call and descended

on the 2000 Hz harmonic (Figure 6b,c). By day 27, in addition to the basic Chirps on each feeding, the chick gave a long but structurally simple call with two dominant harmonics near 1200 and 2400 Hz that were conserved throughout the duration of the call (Figure 6d). We heard a similar call again on day 44 with highly conserved frequencies throughout the duration although with each harmonic about 200 Hz less than the earlier call (Figure 6e). This call resembles the Wail that adults were vocalizing every day in response to overflights of other Red-throated Loons. On day 41, the chick gave a structurally complex call beginning with broad band noise between 1000 and 3000 Hz rising and following about 500 Hz over the broadband noise but then continuing with a single narrow band harmonic near 1100 Hz that gradually ascended to 2000 Hz (Figure 6f). This high amplitude call structurally resembles the Plesiosaur call of the adults and was used by the chick in response to flight solicitation by the adult female.

Vocal responses of the nesting Red-throated Loon pair to other species

Incursions into the nesting territory elicited varying vocal responses by the nesting Red-throated Loon pair (Table 1). The nesting pair responded vocally to 22% of birds that flew over the territory or approached the pair on the water surface ($n = 824$ total interactions resulted in 177 vocal bouts). The pair responded most often to Bald Eagles (42% of responses, 25/59), Common Ravens (25%, 32/129), and Red-throated Loons (22%, 91/405). Among the major vocalizations, Wails were the most frequent, with the highest response rate to Bald Eagle (96% = 24/25 vocal bouts). The Plesiosaur call was given in response to only two species, other Red-throated Loon (34%, 31/91) and Common Loon (38%, 8/21). The Kark was given in response to Bald Eagle, Common Raven, Green-Winged Teal (*Anas crecca*), Red-throated Loon, and Common Loon. Other species that intruded close to the nesting pair's territory, including Red-necked Grebe (*Podiceps griseigena*), Canada Goose (*Branta canadensis*), Green-winged Teal, scaup (*Aythya* sp.), Glaucous-winged Gull (*Larus glaucescens*), and Belted Kingfisher (*Ceryle alcyon*), received little or no vocal response from the nesting pair. Small groups of up to six Canada Goose occasionally swam within 10 m of the nesting loon pair without eliciting an obvious response. In one instance, an adult goose rested for about 5 min on the nesting platform adjacent (20 cm) to the Red-throated Loon incubating eggs, yet the loon showed no behavioural or vocal responses. As well, Red-necked Grebe foraging for fish within the nesting pair's territory ($n = 12$ events) elicited no vocal response or agonistic behaviour.

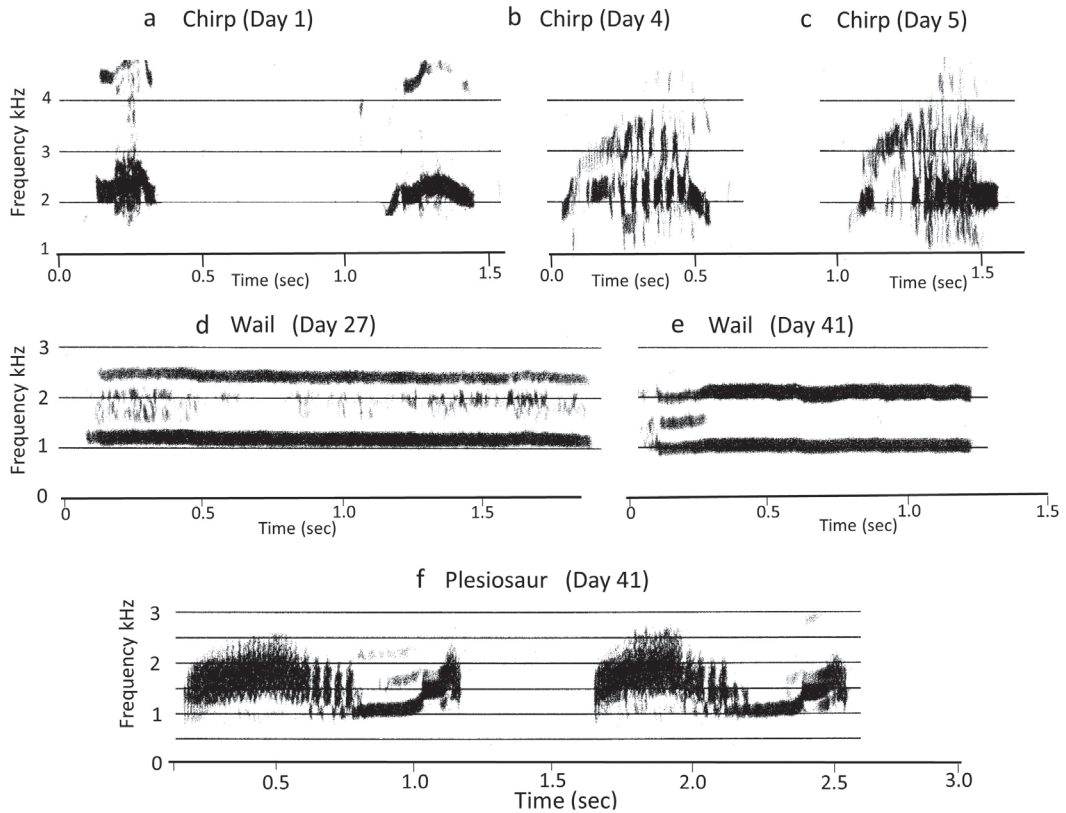


FIGURE 6. Ontogenetic variation in Red-throated Loon (*Gavia stellata*) chick vocalizations on Haida Gwaii, western Canada. a. Chirp (day 1). b. Chirp (day 4). c. Chirp (day 5). d. Wail (day 27). e. Wail (day 41). f. Plesiosaur (Day 41). Bandwidth filter: 150 Hz.

Discussion

Previous documentation of vocalizations in Red-throated Loon from northern Europe defined a repertoire of four calls, consisting of the roll-growl (Plesiosaur), mewling call (Wail), Kark, and cooing call (Coo; Huxley 1923; Keith 1937) while later studies by Sjölander (1977) in Iceland and Alaska added the cackle (Quack). Based on our audio recordings from one nesting pair and observations of numerous nesting and non-breeding pairs of loons from Haida Gwaii, British Columbia, we extend the previous studies and recognize nine calls (Quack, Kark, Wail, Plesiosaur, Coo, Extended Coo, Soft Raack, Loud Raack, and Staccato). Each of the Red-throated Loon calls has multiple harmonics, with the major harmonic between 1000 and 2000 Hz, which is the peak auditory sensitivity of Red-throated Loon (Crowell *et al.* 2015).

The major flight call of Red-throated Loon is the Quack which is used by both territorial and non-breeding pairs. This structurally simple call has no counterpart in other loon species but has some

similarity in sequence, duration, and sound frequency to the ‘Quack’ of Mallard duck (*Anas platyrhynchos*; Abraham 1974), suggesting a common bioacoustical adaptation among groups. Flight calls and timing are closely correlated with wing beat frequency in many bird taxa, including nocturnal flyers, and have a diversity of functions such as social positioning (reviews in La 2011; Berg *et al.* 2019). As well, the calls might act as a ‘vocal altimeter’ given the inner structure of the avian ear that allows sound distances to be estimated (Schnyder *et al.* 2014). Among the Gaviidae, Red-throated Loon has the highest flight requirements, making up to 1000 flights to large lakes or marine waters to obtain food for the young throughout the seven-week pre-fledging period, independent of the presence of fish in the nesting territory (Reimchen and Douglas 1984a). These flights commonly occur during twilight for both nesting and non-breeding birds when visual cues are limited (Reimchen and Douglas 1980) and where a basic flight call is important. Whatever its primary function, the Quack of

Red-throated Loon also acts as a vocal stimulus for territorial vocalizations such as the Wail and Plesiosaur from the lake surface.

The Wail was used by both nesting and non-breeding birds in response to conspecific over-flights. To birds in flight, these Wails could establish an aural map of the surface distribution of individual loons. Such an aural map could be of particular importance in this species because many flights occur at twilight where surface visual cues would be limited (Reimchen and Douglas 1980). The Wail was also used as a high amplitude alarm call by the nesting pair, most consistently in response to overflight or perching of a Bald Eagle, a predator on both young and adult loons in the study area (Douglas and Reimchen 1988a), and to a Common Raven, a potential egg predator (Ewins 1991). Loons did not Wail to territorial incursions of Canada Goose, scaup, Belted Kingfisher, or Red-necked Grebe, none of which are predators or competitors.

The Plesiosaur call and display of Red-throated Loon have been described as “courtship displays” related to establishment of territory and copulation (van Oordt and Huxley 1922; Huxley 1923) and conspecific interactions (Keith 1937). Sjölander (1977) noted that this high intensity call was used most frequently following the return of a partner and in response to conspecifics vocalizing or intruding in the territory, and attributed functions of this call to territorial defence and mate recognition. Our data are generally consistent with this and also show that the Plesiosaur was used when Common Loons entered the nesting territory and by non-breeding pairs that overnighted on the lake (Reimchen and Douglas 1980).

We recognized a group of low amplitude calls used by the nesting adults with their chicks in association with feeding. The calls (Coo, Extended Coo, Staccato, Soft Raack), usually with frequencies less than 1000 Hz, are delivered with varying amplitude and behavioural intensity; the higher intensity Staccato is given when the chicks have not taken the offered fish. Such increased vocal solicitation seems reasonable given the major energetic investment to capture and return the marine fish to the young. In addition to the low amplitude of the calls, the low sound frequencies at the water surface could also be important, as Marten and Marler (1977) have shown experimentally that low frequencies near the ground have high attenuation rates. This is functionally relevant as it would limit the sound transmission to the immediate vicinity of the nest. The much higher amplitude Loud Raack is used by the female to the chick as a flight solicitation to the young near fledging. The Extended Coo has a structure similar to the Wail and can be theoretically transformed into a Wail by damping selected

harmonic frequencies and increasing amplitude. As well, the higher amplitude Loud Raack of the female is structurally derivable from the simple Soft Raack by overall increased frequency and amplitude. We consider these to comprise different calls because of their different behavioural contexts.

Comparisons among species

All loon species have a similar number of high amplitude adult calls, yet the vocal repertoire and call characteristics differ from that of Red-throated Loons. Common Loon and Yellow-billed Loon (*Gavia adamsii*) have three high amplitude calls (Sjölander and Agren 1972, 1976): the Wail and Tremolo, which have variations that are graded in intensity (Barklow 1988, 1979), and the Yodel, a male territorial call with complex structure and context (Mager *et al.* 2010; Mager and Walcott 2014). Arctic Loon (*Gavia arctica*; Sjölander 1978) and possibly Pacific Loon (*Gavia pacifica*; Russell 2020) have a Yodel that resembles Common Loon in structure and variation, the Wail, possibly a low intensity version of the Yodel and the Croak. In comparison, Red-throated Loon have no high amplitude territorial call that resembles the Yodel. Structurally, there are similarities between the Red-throated Loon Wail and sections of the Wail and Yodel of other loons, yet the Red-throated Loon has none of the elaboration and frequency changes of the other species. No other calls have shared characteristics, although there is an overall restriction in calls to frequencies less than 3 kHz and to the use of harmonics. The complex acoustic structure and overlay of noise or sound pulses in the Red-throated Loon Plesiosaur is noticeably lacking in other loons. The Quack, Kark, and Loud Raack have not been reported for other loon species although the Croak of Arctic Loon (Sjölander 1978) may be equivalent. Although vocal repertoires of loon species differ, there are parallels in the behavioural contexts of calls. All five species produced high amplitude vocal responses to extra-pair conspecifics, whether they were intruding into the territory, calling on other territories, or flying over territories. In Common Loons, there is a graded response in the Wail and Tremolo, similar to the escalation of the Wail into the Plesiosaur call and display in Red-throated Loon.

Low amplitude contact calls used by adult pairs in the nesting territory are documented for Common Loon, Yellow-billed Loon, and Arctic Loon (Sjölander 1978; Evers *et al.* 2020; Uher-Koch *et al.* 2020). In our study, we found more complexity than for the other species, recognizing four calls used in different context with the chicks. The lack of specificity of contact calls in the other loon species may simply be a data gap, although the investment that adult Red-throated Loon make in obtaining food for

the young from the ocean, compared to the other loon species, may require a distinct signal to ensure that the young eat.

Ontogeny

Ontogeny of vocalizations over the pre-fledging period in loons has received limited attention. It is best described for Common Loons and ranges from a peep in hatching to adult-like Hoots and Tremolo by eight months and the iconic Yodel by birds older than two years (Evers *et al.* 2020). In our study, pre-fledged Red-throated Loon chicks used Chirps with varying complexity throughout the pre-fledging period, a harmonic call by four weeks, and recognizable Wail and Plesiosaur calls by six weeks just prior to fledging. Although speculative, our sonograms of these vocalizations for two chicks exhibit a large amount of structural variability in the calls that could encode context-specific information for the attending adults.

Duetting

In Red-throated Loons, we documented duetting in the Wail and Plesiosaur in several contexts (pair contact, territory defence) in both the nesting pair and non-breeding birds. Duetting is a habitat-dependent complex co-operative behaviour exhibited by pair-mates (Thorpe 1972 as cited in Malacarne *et al.* 1991; Falls 1982; Farabaugh 1982). Studies of duetting in Common Loon, Yellow-billed Loon, and Pacific Loon have attributed a wide range of functions to the behaviour: alerting partners to threats, distracting potential predators (Barklow 1979), as an alarm call, in territorial conflict (Russell 2020; Uher-Koch *et al.* 2020), and as contact calls in flight (Evers *et al.* 2020). In other studies, defence of a joint resource, such as a breeding territory, is an important function of duetting (Dahlin and Benedict 2014; Brumm and Goyman 2018; Takeda *et al.* 2018; Diniz *et al.* 2019), although functions such as signalling pair-bonds (Farabaugh 1982), paternity guarding (Kahn *et al.* 2018), and facilitating mate recognition (Falls 1982) have been demonstrated as well. In Red-throated Loon, the high intensity coordinated behaviours and high amplitude vocalizations demonstrated in duets may communicate to non-breeding birds and to other territorial pairs both the existence of an occupied territory and the identity of the nesters. With the multiple territories on small ponds and lakes, such as on Haida Gwaii (Douglas and Reimchen 1988b), high amplitude duets may produce an aural map of territories within the region.

Kinematics

The invariable association of Red-throated Loon postures with the Plesiosaur and the Wail indicate that the spatial positioning of the head and neck are involved in specific sound production. The oral

cavity can act like an “oral bell”, reducing impedance as sound transfers from the pharynx to the outside air (Gaunt *et al.* 1987); this is a likely explanation for the distended “pouch” below the base of the bill seen in the Plesiosaur posture. Distention of the neck in the Wail and the Plesiosaur call suggests an anatomical modification producing a resonant chamber, a mechanism for call amplification used by some grouse, curassows (Wiley and Richards 1982), and ducks (Brackenbury 1982). Bill gape has been found to modulate frequency in passerines (Westneat *et al.* 1993) and in geese (Hausberger *et al.* 1991). Some of these processes may be involved in the modification of calls by physical displays in Red-throated Loon.

Characteristics of the avian trachea (length, diameter, and thickness) affect the sound generated by the internal tympaniform membranes by amplifying or damping frequencies (see Brackenbury 1982 for review). Sutherland and McChesney (1965) concluded that calls in Ross’ Goose (*Chen rossii*) and Snow Goose (*Chen caerulescens*) were both modulated by tracheal resonance and that the difference between the two species is related to differing tracheal length. Greenewalt (1968) analyzed the harmonics in calls of Whooping Crane (*Grus americana*), Whistling Swan (*Olor columbianus*), and Trumpeter Swan (*Cygnus buccinator*), all of which have exceptionally long tracheae coiled at their base, and found no relationship between tracheal length and harmonic frequencies. There is no evidence of tracheal coiling in Gaviidae. We found that in some of the Red-throated Loon calls (Wail, Quack, Kark, and female Plesiosaur call) the lowest harmonic was not equivalent to the intervals between the harmonics; that is, the lowest harmonic frequency was not the fundamental. In the Wail, series of harmonics both higher and lower than the dominant frequencies were completely damped in parts of the call. This, in association with display kinematics, indicates that there is considerable modulation of song characteristics, which could mean more transmission of greater content and individual information in calls.

Sexual dimorphism

Sexual dimorphism in avian vocalizations is common and represents two processes: differences in the type of calls by each sex and differences in the acoustic structure of individual calls. Both processes are known in Gaviidae. In Common Loon and Yellow-billed Loon, only the male gives the Yodel, the dominant territorial call (Sjölander and Agren 1972, 1976; Walcott *et al.* 2006). Although we have previously shown that male Red-throated Loon are largely responsible for defense, including direct attacks on intruders (Reimchen and Douglas 1985), we have not identified any male-specific vocalization associated

with territoriality defense. Rather, the Wail, the most prevalent territorial call, is given by male or female either singly or in duet. Vocalizations directed to the chicks differed between the sexes for some calls, as the Coo and Extended Coo were only recorded for the male and the Low Raack for the female, although they had similar contexts in interacting with the young and each other in the nesting territory and feeding fish to the young.

Sex differences in acoustic structure of the calls have also been reported for other loon species. In Common Loon and Yellow-billed Loon, the Tremolo, the major flight call, is lower pitched in the male than in the female (Sjölander and Agren 1976), possibly associated with body size because male loons are about 10% larger than females in each species (Selander 1966; Cramp and Simmons 1977). Our acoustic data on Red-throated Loon are similar as we found that in both the Wail and the Plesiosaur, the male vocals were about 200–400 Hz lower than that of the female. We cannot assess whether this difference is a by-product of the body size or more context-specific behaviour differences in the interactions with the chicks.

Alarm calls

For species exposed to multiple predators, alarm calls distinct for each predator group would provide improved response options of the target prey (e.g., Leger *et al.* 1980; Templeton 2005). Throughout the geographical nesting range, loons overlap with a range of egg and chick predators including ravens, gulls, skuas, jaegers, foxes, wolves, and raptors (Johnson and Johnson 1935; Cyrus 1975; Bundy 1976; Furness 1983) and this might predict species-specific vocal responses. We observed that Red-throated Loon exhibited several distinctive alarm calls to predators such as the Kark towards Common Raven, which is an egg predator (Ewins 1991), and the Kark and Wail towards Bald Eagles. Solitary eagles were present in the study area almost daily throughout summer and have attacked Red-throated Loon chicks as well as adults (Douglas and Reimchen 1988b). We also observed that when chicks were present, the adult Red-throated Loon responded aggressively with the Wail or Kark to both other Red-throated Loon and Common Loon, as these are known to attack Red-throated Loon chicks in the territory (Reimchen and Douglas 1985). There were no vocal responses to the multiple avian taxa that were not a threat to the pre-fledged young.

Conclusion

Our observations of nesting and non-nesting Red-throated Loon show a diversity of vocalizations and variable responses to intra- and interspecies interactions. The Quack and the Plesiosaur are two calls that are unique to Red-throated Loon. While it is possible

that these calls represent ancestral traits in this basal taxon, it is equally or more probable that their vocal repertoire is an acoustical adaptation to the distinctive life history of nesting in small lakes or ponds that require flights to and from the territory throughout the pre-fledging period. We identified nine calls, more than previously reported, but feel these might still be over-simplified categories that greatly underestimate the complexity of their vocal repertoire, given the multiple instances of context-specific behavioural responses to different vocalizations. While our data on acoustic structure are limited to a single nesting pair, these represent the first characterization of this dimorphism in Red-throated Loon and provide a basis for future comparisons. The extent to which these vocalizations comprise syntactical and referential signals (review in Smith 2017) awaits further study.

Author Contributions

Writing – Original Draft: S.D.D.; Writing, Review & Editing: T.E.R. and S.D.D.; Conceptualization: S.D.D. and T.E.R.; Investigation: S.D.D. and T.E.R.; Methodology and Analyses: S.D.D. and T.E.R.; Visualization: S.D.D. and T.E.R.

Acknowledgements

We thank C. Pazskowski and S. Hannon for discussion and E.H. Miller, L.Y. Zanette, M.J. Clinchy, and three reviewers for constructive comments on the manuscript. We are also grateful to E.H. Miller and J.B. Foster for audio recording equipment, and to J.T. Hogan for assistance with the sound sonogram. We acknowledge the Macaulay Library at the Cornell Lab of Ornithology for storage and accessibility of the Red-throated Loon vocalizations. This research was supported by the Ecological Reserves Unit, Ministry of the Environment, Government of British Columbia, the Vancouver Public Aquarium, and a Natural Sciences and Engineering Research Council operating grant to T.E.R. (NRC2354).

Literature Cited

- Abraham, R.L. 1974. Vocalizations of the Mallard (*Anas platyrhynchos*). *Condor* 1974: 401–420. <https://doi.org/10.2307/1365814>
- Barklow, W.E. 1979. Graded frequency variations of the tremolo call of the Common Diver (*Gavia immer*). *Condor* 81: 53–64. <https://doi.org/10.2307/1367857>
- Barklow, W.E. 1988. The structure and function of the wail call of the Common Loon. Page 53 in *Papers from the 1987 Conference on Common Loon Research and Management*. Edited by P.I.V. Strong. North American Loon Fund, Meredith, New Hampshire, USA.
- Barr, J.F., C. Eberl, and J.W. McIntyre. 2000. Red-throated Loon (*Gavia stellata*), version 2.0. In *The Birds of North America*. Edited by A.F. Poole and F.B. Gill.

- Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bna.513>
- Berg, K.S., S. Delgado, and A. Mata-Betancourt.** 2019. Phylogenetic and kinematic constraints on avian flight signals. *Proceedings of the Royal Society B: Biological Sciences* 286: 20191083. <https://doi.org/10.1098/rspb.2019.1083>
- Brackenbury, J.H.** 1982. The structural basis of voice production and its relationship to sound characteristics. Pages 53–71 in *Acoustic Communication in Birds, Volume 1*. Edited by D.H. Kroodmsa and E.H. Miller. Academic Press, New York, New York, USA.
- Brumm, H., and W. Goymann.** 2018. The function of collective signalling in a cuckoo. *Animal Behaviour* 146: 23–30. <https://doi.org/10.1016/j.anbehav.2018.10.008>
- Bundy, G.** 1976. Breeding biology of Red-throated Diver. *Bird Study* 23: 249–256. <https://doi.org/10.1080/00063657609476511>
- Catchpole, C.K.** 1982. Evolution of bird sounds in relation to mating and spacing behaviour. Pages 297–319 in *Acoustic Communication in Birds, Volume 1*. Edited by D.H. Kroodmsa and E.H. Miller. Academic Press, New York, New York, USA.
- Cramp, S., and K.E.L. Simmons.** 1977. Pages 43–49 in *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic, Volume 1*. Oxford University Press, Oxford, United Kingdom.
- Crowell, S.E., A.M. Wells-Berlin, C.E. Carr, G.H. Olsen, R.E. Therrien, S.E. Yannuzzi, and D.R. Ketten.** 2015. A comparison of auditory brainstem responses across diving bird species. *Journal of Comparative Physiology A* 201: 803–815. <https://doi.org/10.1007/s00359-015-1024-5>
- Cyrus, D.G.** 1975. Breeding success of Red-throated Divers on Fetlar. *British Birds* 68: 75–76.
- Dahlin, C.R., and L. Benedict.** 2014. Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. *Ethology* 1220: 1–10. <https://doi.org/10.1111/eth.12182>
- Diniz, P., R.H. Macedo, and M.S. Webster.** 2019. Duetting correlates with territory quality and reproductive success in a subsocial bird with low extra-pair paternity. *Auk* 136: 1–13. <https://doi.org/10.1093/auk/uky004>
- Douglas, S.D., and T.E. Reimchen.** 1988a. Habitat characteristics and population estimate of breeding Red-throated Loons (*Gavia stellata*) on the Queen Charlotte Islands. *Canadian Field-Naturalist* 102: 679–684. Accessed 10 June 2021. <https://www.biodiversitylibrary.org/page/28243956>.
- Douglas, S.D., and T.E. Reimchen.** 1988b. Reproductive phenology and early survivorship in Red-throated Loons (*Gavia stellata*). *Canadian Field-Naturalist* 102: 701–704. Accessed 10 June 2021. <https://www.biodiversitylibrary.org/page/28243978>.
- Evers, D.C., J.D. Paruk, J.W. McIntyre, and J.F. Barr.** 2020. Common Loon (*Gavia immer*), version 1.0. In *Birds of the World*. Edited by S.M. Billeraman. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.comloo.01>
- Ewins, P.J.** 1991. Egg predation by corvids in gull colonies on Lake Huron. *Colonial Waterbirds* 14: 186–189. <https://doi.org/10.2307/1521511>
- Falls, J.B.** 1982. Individual recognition by sounds in birds. Pages 237–278 in *Acoustic Communication in Birds, Volume 2*. Edited by D.H. Kroodmsa and E.H. Miller. Academic Press, New York, New York, USA.
- Farabaugh, S.M.** 1982. The ecological and social significance of duetting. Pages 85–124 in *Acoustic Communication in Birds, Volume 2*. Edited by D.H. Kroodmsa and E.H. Miller. Academic Press, New York, New York, USA.
- Furness, R.W.** 1983. Foula, Shetland, Volume 4. *Birds of Foula*. The Brathay Hall Trust, Ambleside, Cumbria, United Kingdom.
- Gaunt, A.S., S.L.L. Gaunt, H.D. Prange, and J.S. Wasser.** 1987. The effects of tracheal coiling on the vocalizations of cranes (Aves; Gruidae). *Journal of Comparative Physiology A* 161: 43–58. <https://doi.org/10.1007/bf00609454>
- Greenewalt, C.H.** 1968. *Bird Song: Acoustics and Physiology*. Smithsonian Institution Press, Washington, DC, USA.
- Hausberger, M., J.M. Black, and J.-P. Richard.** 1991. Bill opening and sound spectrum in barnacle goose loud calls: individuals with ‘wide mouths’ have higher pitched voices. *Animal Behaviour* 42: 319–322. [https://doi.org/10.1016/S0003-3472\(05\)80565-2](https://doi.org/10.1016/S0003-3472(05)80565-2)
- Huxley, J.S.** 1923. Courtship activities in the Red-throated Diver (*Colymbus stellatus* Pontopp); together with a discussion of the evolution of courtship in birds. *Zoological Journal of the Linnaean Society* 35: 253–292. <https://doi.org/10.1111/j.1096-3642.1923.tb00048.x>
- Johnson, R.A., and H.A. Johnson.** 1935. A study of the nesting and family life of the Red-throated Loon. *Wilson Bulletin* 47: 97–103.
- Kahn, Z.A., C. Moser-Purdy, and D.J. Mennill.** 2018. Sing and do not stray: male rufous-and-white wrens use duets and physical behaviours to guard their mates. *Animal Behaviour* 143: 35–42. <https://doi.org/10.1016/j.anbehav.2018.07.005>
- Keith, D.B.** 1937. The Red-throated Diver in North East Land. *British Birds* 31: 66–81.
- La, V.T.** 2011. Diurnal and nocturnal birds vocalize at night: a review. *Condor* 114: 245–257. <https://doi.org/10.1525/cond.2012.100193>
- Leger, D.W., D.H. Owings, and D.L. Gelfand.** 1980. Single note vocalizations of California ground squirrels: graded signals and situation-specificity of predator and socially evoked calls. *Zeitschrift für Tierpsychologie* 52: 227–246. <https://doi.org/10.1111/j.1439-0310.1980.tb00714.x>
- Mager, J.N., and C. Walcott.** 2014. Dynamics of an aggressive vocalization in the Common Loon (*Gavia immer*): a review. *Waterbirds* 37: 37–46. <https://doi.org/10.1675/063.037.sp106>
- Mager, III, J.N., C. Walcott, and W.H. Piper.** 2010. Common Loons can differentiate yodels of neighboring and non-neighboring conspecifics. *Journal of Field Ornithology* 81: 392–401. <https://doi.org/10.1111/j.1557-9263.2010.00295.x>
- Malacarne, G., M. Cucco, and S. Camanni.** 1991. Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds. *Ethology Ecology & Evolution* 3: 207–219. <https://doi.org/10.1080/08927014.1991.9525369>

- Marten, K., and P. Marler.** 1977. Sound transmission and its significance for animal vocalization: I. Temperate Habitats. *Behavioral Ecology and Sociobiology* 2: 271–290. <https://doi.org/10.1007/bf00299740>
- Reimchen, T.E., and S.D. Douglas.** 1980. Observations of loons (*Gavia immer* and *G. stellata*) at a bog lake on the Queen Charlotte Islands. *Canadian Field-Naturalist* 94: 398–404. Accessed 10 June 2021. <https://www.biodiversitylibrary.org/page/28089295>.
- Reimchen, T.E., and S.D. Douglas.** 1984a. Feeding schedule and daily food consumption in Red-throated Loons (*Gavia stellata*) over the pre-fledging period. *Auk* 101: 593–599. <https://doi.org/10.1093/auk/101.3.593>
- Reimchen, T.E., and S.D. Douglas.** 1984b. Seasonal and diurnal abundance of aquatic birds on the Drizzle Lake Reserve, Queen Charlotte Islands, British Columbia. *Canadian Field-Naturalist* 98: 22–28. Accessed 10 June 2021. <https://www.biodiversitylibrary.org/page/28063849>.
- Reimchen, T.E., and S.D. Douglas.** 1985. Differential contribution of the sexes to pre-fledged young in Red-throated Loons. *Auk* 102: 198–201. <https://doi.org/10.2307/4086848>
- Reimchen, T.E., and S.D. Douglas.** 2021. Loon abundance and behaviour over four decades at a remote ecological reserve on Haida Gwaii, British Columbia, Canada. *Canadian Field-Naturalist* 135: 28–38. <https://doi.org/10.22621/cfn.v135i1.2617>
- Rizzolo, D.J., C.E. Gray, J.A. Scmutz, J.F. Barr, C. Eberly, and J.W. McIntyre.** 2020. Red-throated Loon (*Gavia stellata*), version 2.0. In *Birds of the World*. Edited by P.G. Rodewald and B.K. Keeney. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.retloo.02>
- Rummel, L., and C. Goetzinger.** 1975. The communication of intraspecific aggression in the Common Loon. *Auk* 92: 333–346. <https://doi.org/10.2307/4084561>
- Russell, R.W.** 2020. Pacific Loon (*Gavia pacifica*), version 1.0. In *Birds of the World*. Edited by P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.pacloo.01>
- Schnyder, H.A., D. Vanderelst, S. Bartenstein, U. Firzloff, and H. Luksch.** 2014. The avian head induces cues for sound localization in elevation. *PLoS ONE* 9: e112178. <https://doi.org/10.1371/journal.pone.0112178>
- Selander, R.K.** 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113–151. <https://doi.org/10.2307/1365712>
- Selous, E.** 1912. An observational diary on the domestic habits of the red-throated diver (*Colymbus septentrionalis*). *Zoologist* 849: 81–96, 171–180, 210–219.
- Sjölander, S.** 1977. On the behaviour of the Red-throated Diver, *Gavia stellata*, during reproduction. Unpublished report, Bielefeld University, Bielefeld, Germany.
- Sjölander, S.** 1978. Reproductive behaviour of the Black-Throated Diver *Gavia arctica*. *Ornis Scandinavica* 9: 51–65. <https://doi.org/10.2307/3676139>
- Sjölander, S., and G. Agren.** 1972. Reproductive behaviour of the Common Loon. *Wilson Bulletin* 84: 296–308.
- Sjölander, S., and G. Agren.** 1976. Reproductive behaviour of the Yellow-billed Loon *Gavia adamsii*. *Condor* 78: 454–463. <https://doi.org/10.2307/1367094>
- Smith, C.L.** 2017. Referential signalling in birds: the past, present and future. *Animal Behaviour* 124: 315–323. <https://doi.org/10.1016/j.anbehav.2016.08.015>
- Sprengelmeyer, Q.D.** 2014. A phylogenetic reevaluation of the genus *Gavia* (Aves: Gaviformes) using next-generation sequencing. M.Sc. thesis, Northern Michigan University, Marquette, Michigan, USA. Accessed 10 June 2021. <https://commons.nmu.edu/theses/1>.
- Sutherland, C.A., and D.S. McChesney.** 1965. Sound production in two species of geese. *Living Bird* 4: 99–106.
- Suzuki, T.N.** 2016. Semantic communication in birds: evidence from field research over the past two decades. *Ecological Research* 31: 307–319. <https://doi.org/10.1007/s11284-016-1339-x>
- Takeda, K.F., M. Hiraiwa-Hasegawa, and N. Kutsukake.** 2018. Duet displays within a flock function as a joint resource defence signal in the red-crowned crane. *Behavioural Ecology and Sociobiology* 72: 66. <https://doi.org/10.1007/s00265-018-2485-7>
- Templeton, C.W.** 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* 308: 1934–1937. <https://doi.org/10.1126/science.1108841>
- Uher-Koch, B.D., M.R. North, and J.A. Schmutz.** 2020. Yellow-billed Loon (*Gavia adamsii*), version 1.0. In *The Birds of the World*. Edited by S.M. Billerman. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.yebloo.01>
- van Oordt, G.J., and J.S. Huxley.** 1922. Some observations on the habits of the Red-throated Diver in Spitsbergen. *British Birds* 16: 34–36.
- Walcott, C., J.N. Mager, and W. Piper.** 2006. Changing territories, changing tunes: male loons, *Gavia immer*, change their vocalizations when they change territories. *Animal Behaviour* 71: 673–683. <https://doi.org/10.1016/j.anbehav.2005.07.011>
- Walcott, C., D.C. Evers, M. Froehler, and A. Krakauer.** 1999. Individuality in “yodel” calls recorded from a banded population of Common Loons, *Gavia immer*. *Bioacoustics* 10: 101–114. <https://doi.org/10.1080/09524622.1999.9753424>
- Westneat, M.W., J.H. Long, W. Hoese, and S. Nowicki.** 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic feature in sparrows. *Journal of Experimental Biology* 182: 147–171. <https://doi.org/10.1242/jeb.182.1.147>
- Wiley, R.H., and D.G. Richards.** 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pages 132–176 in *Acoustic Communication in Birds*, Volume 1. Edited by D.H. Kroodsma and E. H. Miller. Academic Press, New York, New York, USA.
- Wilson, D.R., and C.S. Evans.** 2012. Fowl communicate the size, speed and proximity of avian stimuli through graded structure in referential alarm calls. *Animal Behaviour* 83: 535–544. <https://doi.org/10.1016/j.anbehav.2011.11.033>

Received 12 June 2020

Accepted 10 June 2021

Associate Editor: J.R. Foote

APPENDIX 1. Accession numbers for representative audio-recordings and spectrograms of Red-throated Loons (*Gavia stellata*) at Drizzle Lake, Haida Gwaii, western Canada uploaded to the Macaulay Library at the Cornell Lab of Ornithology (<https://macaulaylibrary.org>). Recordings were made by S.D.D. and T.E.R. and are part of the data used in this study. Spectrograms accompanying the recordings were produced by the Macaulay Library.

Call	Hyperlink	Accession number
Adult pair with 1-day old chick	https://macaulaylibrary.org/asset/221326721	ML221326721
Kark	https://macaulaylibrary.org/asset/221510911	ML221510911
Wail and Plesiosaur, male and female duet	https://macaulaylibrary.org/asset/216337511	ML216337511
Plesiosaur, male and female duet	https://macaulaylibrary.org/asset/216348661	ML216348661
Quack	https://macaulaylibrary.org/asset/216351121	ML216351121
Loud Raack	https://macaulaylibrary.org/asset/221524591	ML221524591