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Variation in the Vocal Behavior of Common Loons (*Gavia immer*): Insights from Landscape-level Recordings

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Abstract.—Animal signals play an important role in mate attraction and territory defense, and animals may benefit by adopting signaling strategies that maximize effective communication in the face of changing environmental conditions. In this study, a custom-designed microphone array was used to collect landscape-scale recordings of the acoustic signaling behavior of Common Loons (*Gavia immer*) along a 10-km transect spanning three lakes in eastern Ontario, Canada. Recordings were collected during the early part of the breeding season during two consecutive years (2008-2009). Analyses focused on understanding how the vocal output of Common Loons varied with time of day, time of year, and in response to variation in weather. Common Loons showed significant diel variation in vocal output, producing more *wail*, *yodel*, and *tremolo* calls at night than during the day. Common Loons showed significant seasonal variation in vocal output, producing fewer *wail*, *yodel*, and *tremolo* calls as the first month of the breeding season progressed. Common Loons showed significant differences in vocal behavior with changing weather conditions, producing more calls at cold temperatures, with low wind speed and air pressure, and when rain was light or absent. Microphone array recordings were used to estimate signal transmission properties of Common Loon vocalizations, demonstrating that *wail*, *yodel*, and *tremolo* calls transmit significantly farther at night than during the day. These results provide quantitative details of Common Loon vocal signaling strategies, revealing that this species calls when abiotic conditions are ideal for long-range signaling. *Received 4 February 2013, accepted 29 May 2013.*

Key words.—Acoustic monitoring, active signal space, Common Loon, diel variation, *Gavia immer*, microphone array, seasonal variation, signaling strategies, sound transmission, vocalizations.

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Animals change their behavior in response to variation in their environment. Exploring the relationship between behavioral and environmental variation provides insight into the ecology and ethology of free-living animals (Bradbury and Vehrencamp 2011). The acoustic behavior of birds provides an excellent example of a conspicuous behavioral trait that varies in relation to abiotic factors (Catchpole and Slater 2008). Vocalizations in birds often play a critical role in mate attraction and territory defense, and birds may find both naturally selected and sexually selected benefits by adopting signaling strategies that maximize effective communication in a changing environment.

Many birds exhibit notable circadian and circannual variation in their acoustic behavior. The complex vocalizations of many diverse bird species show a pronounced annual pattern where signals that are important in territory defense and mate attraction are produced in abundance early in the breeding season, but are rare or absent at other times of year (e.g., Slagsvold 1977). Many birds also exhibit a pattern of diel variation where vocal output reaches its maximum in the twilight of dawn or, less commonly, the twilight of dusk (reviewed in Staicer *et al.* 1996). In addition to daily and seasonal variation, the vocal behavior of birds also varies with climatic conditions. In conditions of rain or high wind, for example, acoustic signaling is an inefficient behavior because of the masking effects of rain and degradation due to wind (Brumm and Slabbekoorn 2005). Studies of many unrelated species show that animals facilitate communication by changing their signaling location (e.g., Blumenrath and Dabelsteen 2004; Barker and Mennill 2009) or the timing of signal production (e.g., Brumm 2006; Fuller *et al.* 2007). Such signaling strategies can benefit animals by enhancing signal transmission and leading to more effective communication (Brumm and Naguib 2009).

Common Loons (*Gavia immer*) produce iconic sounds of northern lakes and are well known for their far-carrying vocalizations. Given the scale of their communication, with calls thought to transmit many kilometers between signaler and receiver (Olson and Marshall 1952; Evers *et al.* 2010), Common Loons provide a particularly interesting case study for exploring the relationship between vocal behavior and abiotic factors. More so than most animals whose vocalizations transmit over tens or hundreds of meters, Common Loons may be particularly sensitive to abiotic factors that influence the transmission of their calls.

Common Loons produce a variety of vocalizations. In this investigation, I focus on four call types that have been described in prior investigations (see Fig. 1). *Wail* calls are medium-length howling notes produced by both sexes, known to function as a contact call between mates and during agonistic territorial interactions (Evers *et al.* 2010). *Yodel* calls are long, complex, frequency-modulated calls produced by males. *Yodels* are individually distinctive (Walcott *et al.* 1999; Mager *et al.* 2010; see also Walcott *et al.* 2006), are associated with aggressive territorial interactions on the breeding grounds (Rummel and Goetzinger 1975), and are understood to be honest signals of male size, condition, and motivation (Mager *et al.* 2007, 2012). *Tremolo* calls are short, laughing phrases produced by both males and females, and are known to function as alarm calls and territorial calls (Barklow 1979). *Hoot* calls are short, quiet notes given by both males and females, and are understood to play a role in maintaining contact between breeding partners or between parents and their offspring (Evers *et al.* 2010).

In this study, my goal was to explore variation in the vocal behavior of Common Loons in terms of circadian patterns, seasonal patterns, and patterns related to weather. I also sought to determine whether Common Loon vocalizations show different transmission patterns during the day vs. night. Previous investigations suggest that some Common Loon calls change in output as the season progresses and that their vocalizations are more common at night (Rummel and Goetzinger 1975; Wentz 1990), and I sought to confirm whether this was true based on quantitative evidence. As far as I am aware, no previous publication has quantified variation in Common Loon vocal output due to variation in weather, or systematically quantified variation in vocal output by time of day or time of breeding season.

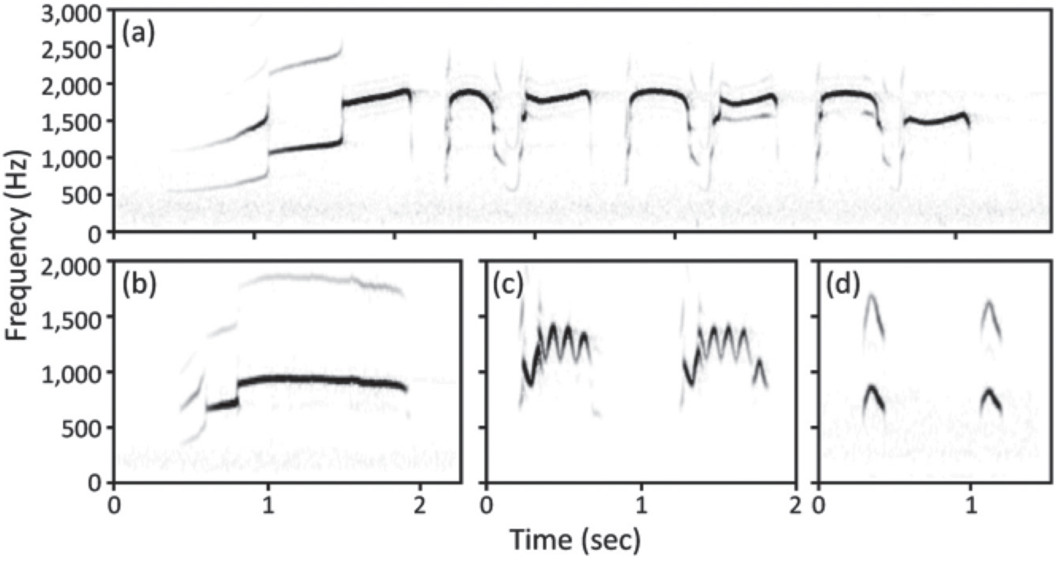

Figure 1. Sound spectrograms depicting four common types of Common Loon vocalizations: (a) a *yodel* call, (b) a *wail* call, (c) two *tremolo* calls, and (d) two *hoot* calls.

METHODS

Study Site and Field Methods

I recorded Common Loons (hereafter "loons") living on the lakes surrounding Queen's University Biological Station north of Kingston, Ontario, Canada (44° 34' N, 76° 19' W). The study site comprised three freshwater lakes: Lake Opinicon, Lower Rock Lake, and Upper Rock Lake (Fig. 2). Loon recordings were collected between late April and late May in 2008 and 2009 several weeks after the loons arrived on the breeding grounds, during their early breeding season (egg laying in Ontario occurs in mid- to late May; Evers *et al.* 2010).

Loons were monitored from a distance by canoe to map the primary activity area for each focal pair. The study population was not individually marked. Loons are long-lived and occupy the same territories for extended periods (McIntyre 1988; Evers *et al.* 1996). Thus, I assumed that the same pairs were resident in the area throughout the recording period. Analysis of the spectrograms of the individually distinctive male *yodel* calls supported this assumption and suggested that the same males were present in the same territories in both years of the study. During field observations, any evidence of nesting activity was noted (e.g., birds collecting nesting material).

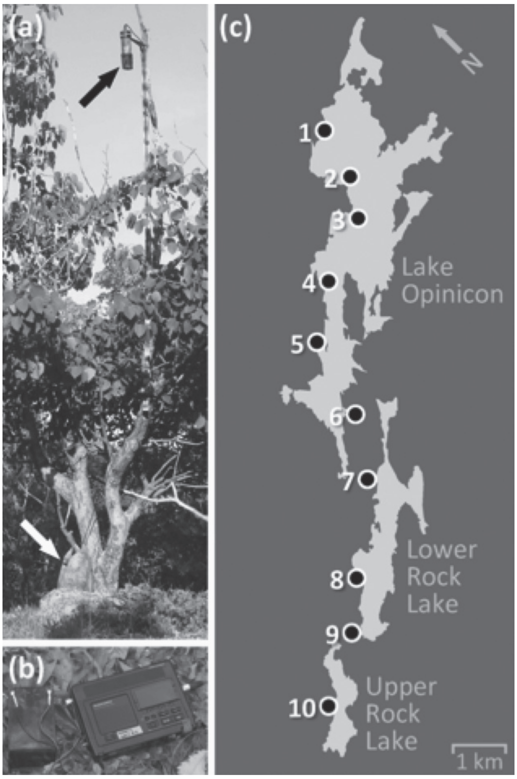

Figure 2. Automated digital recorders used to sample vocalizations from Common Loons along a 10-km transect in eastern Ontario. (a) A photograph showing one recording device, with arrows indicating the microphone (top) and the recording device housed in a waterproof dry bag (bottom). (b) A digital recorder and a battery. (c) A map of the array of 10 digital recorders. The array was positioned along a near-linear transect, with recorders approximately 1 km apart, spanning three freshwater lakes near Queen's University Biological Station in Ontario, Canada.

Recording Apparatus

I sampled loon vocalizations with an array of 10 custom-designed autonomous recorders, each capable of recording continuously for 24 hr (Fig. 2). Each device included an omnidirectional microphone (Sennheiser ME-62/K6; frequency response: 30-20,000 Hz) connected to a digital sound recorder (Marantz PMD-670) that was powered by an external sealed lead-acid battery. Microphones were mounted at a height of 3 m on wooden poles that were lashed to the trunks of small trees. The microphone was suspended 30 cm from the pole with a shelf bracket. The omnidirectional microphone was protected from rain by a 7.5-cm diameter polyvinyl-chloride (PVC) cap, and a wind screen baffle surrounding the microphone. The recorder and battery were protected from rain in a dry bag lashed to the base of the tree.

The 10 recorders were positioned near the shorelines of the three study lakes. Each recorder was visited on a daily basis so that the battery and memory card could be changed. The recordings were time-stamped each day by a recordist who read aloud the time from a handheld Global Positioning System (GPS) device, using a dog clicker to note the specific seconds from the GPS clock; the voice of the recordist and these *clicks* served as reference sounds for synchronizing the 10 recordings later in the laboratory. Due to the limited size of the memory cards, recordings were collected as MP3 files (16-bit sampling, 22,050 Hz) and later converted to larger Audio Interchange Format files (AIF) for analysis in the laboratory (AIF files, but not MP3 files, were compatible with the sound analyses detailed below).

I arranged the 10 recorders in a near-linear array along the shorelines of the three study lakes where adjacent recorders were separated by approximately 1 km (Fig. 2). This system allowed me to monitor simultaneously the vocalizations from loons on all three lakes. Based on the simultaneous recordings, I estimated the position of a vocalizing loon by comparing the sound arrival time at each of the recorders. Because of the clock drift in the independent recorders, these recordings did not facilitate triangulation as in other microphone array systems (e.g., Mennill *et al.* 2006, 2012). However, given the 1-km spacing between microphones, it was easy to assign vocalizations to an animal near one of the 10 recorders based on sound arrival time as well as the amplitude of the recorded calls. Uniquely, this recording system facilitated the estimation of transmission distances of the three long-distance calls of loons (*wails*, *yodels*, and *tremolos*) by investigating how many microphones in the array detected a call from an animal of known position.

Acoustic Analysis

In the laboratory, sound spectrograms of the 24-hr sound files were visualized using Syrinx-PC (Burt 2008). I used Syrinx-PC as a multi-channel browser to visualize the 10 recordings simultaneously, relying on the GPS time in each recording to synchronize the 10 single-channel recordings. Recordings were scanned visually, and all loon vocalizations of the four types described above were annotated. I focused my analysis on 28 24-hr periods where the 10 microphones were deployed successfully (10 24-hr periods in 2008; 18 24-hr periods in 2009), producing 6,720 hr of one-channel recordings, or 672 hr of 10-channel recordings.

Field observations confirmed that each microphone was located near the center of the territory of a different pair of loons. As such, my study population was 10 loon territories (i.e., the territory in the immediate vicinity of each of the 10 recorders). For vocalizations that were detected by multiple recorders, vocalizations were assigned to one of the 10 loon territories by noting which microphone recorded the vocalization with the highest amplitude and with the earliest arrival time (given the spherical spreading of sound, signals should reach closer microphones sooner, with an approximate delay of 3 sec for a sound to transmit 1 km between adjacent recorders). Calls from distant loons were also recorded with the microphone array (particularly near microphones 1 and 2, which were closest to additional lakes and loon territories), but they were of notably lower amplitude. Calls from outside the 10 focal territories were not included in the analysis.

Sound Transmission Measurements

In addition to studying variation in vocal output from the 10 territories, I used the microphone array recordings to study the transmission properties of loon vocalizations in the day (the period between sunrise and sunset) vs. night (the period between sunset and sunrise). I used the number of recorders in the array that detected a call as a proxy for estimating the radius of a vocalization's signal space. To accomplish this, I focused on examples of vocalizations that unambiguously originated from one of the 10 focal loon territories. For each vocalization, I evaluated how many other microphones in the array recorded the sound, moving away from the vocalizing animal's position in one direction along the linear array, toward the center of the array, to maximize opportunity for detection by the other microphones. I counted the number of adjacent recording sites where the call was visually detectable on the sound spectrogram in Syrinx-PC, changing the gain levels in Syrinx-PC to confirm that the vocalization was not detected even at higher spectral gain values. Each of the 10 recorders consisted of identical equipment with identical recording settings so that each of the units was equally capable of detecting loon vocalizations. With microphones separated by approximately 1 km, these estimates provided a rough proxy for the transmission distance of loon vocalizations. Landscape features might influence transmission characters differently across the 10-km transect, but I conducted the analyses pair-wise for each of the 10 recording sites so that landscape features would similarly influence transmission properties during day or night. Substantial error was noted in these calculations because the position of the vocalizing animal was only known to within 1 km; nevertheless, this technique allowed me to approximate the amount of daytime vs. nighttime communication in loons.

I collected transmission measurements for 10 daytime and 10 nighttime examples of *wails*, *yodels*, and *tremolos* for each of the 10 focal territories. (Given their low amplitude and short transmission distances, *hoots* were not included in this analysis; *hoots* were usually detected by a single recorder within the linear array.) For each of the three types of calls, I collected daytime transmission measurements from 10 calls recorded between 10:00 and 15:00 hr, and nighttime transmission measurements from 10 calls recorded between 22:00 and 03:00 hr. I made only one daytime and nighttime measurement of each call type at each microphone per 24-hr recording period. I then computed the average transmission distance calculation for all 10 daytime and nighttime measurements per call type for each of the 10 territories.

Weather Data Collection

Weather data were collected from a weather station (Campbell Scientific, Logan, UT) at Queen's University Biological Station, facilitating a comparison with local, site-specific climatic conditions (the weather station was located on Lake Opinicon within the recording area near microphone 3 in Fig. 2). I focused on six weather variables. Air temperature (°C), relative humidity (%), air pressure (kPa), and wind speed (m/s) were measured every 6 sec, and then converted to hourly averages. Rainfall (mm) and water temperature (°C; measured at a depth of 0.2 m in the waters of Lake Opinicon) were measured hourly.

Statistical Analysis

I analyzed both diel variation and seasonal variation in the vocal output of loons using linear mixed models. The fixed factors included time (24 1-hr time bins), Julian day (28 days sampled between 25 April and 28 May), the interaction between time and Julian day, and year (2008 or 2009). I included recording location (10 sites) as a random effect to account for the same 10 sites being sampled repeatedly. I conducted four separate models, one for each of the four types of vocalizations. I estimated fixed effects following the restricted maximum likelihood method. To compare directly the number of calls at night vs. day, I conducted paired t-tests on the average number of each type of call per night and per day over the entire recording period. I also used paired t-tests to analyze daytime vs. nighttime transmission characteristics of *wails*, *yodels*, and *tremolos*.

To analyze the influence of weather on the vocal output of loons, I used linear mixed models. The fixed factors included six weather variables (listed above) and year (2008 or 2009). Again, I included recording location as a random effect, I conducted a separate model for each of the four types of vocalization, and I estimated fixed effects using the restricted maximum likelihood method. For the analysis of weather, I focused on vocalizations produced between 22:00 to 03:00 hr, when loons are most vocal (see below). All analyses were conducted in JMP (SAS Institute, Inc., 2013). Values are presented as means ± SE. All tests are two-tailed.

RESULTS

Variation in Vocal Output with Time of Day

Loon vocal output varied with time of day (Fig. 3). Within each 24-hr cycle, loons showed significant variation in *wails* (Fig. 3a; time-of-day fixed factor in the linear mixed model: $F_{1,6706} = 90.7$, $P < 0.001$), *yodels* (Fig. 3b; $F_{1,6706} = 18.8$, $P < 0.001$), and *tremolos* (Fig. 3c; $F_{1,6706} = 54.4$, $P < 0.001$). Output of *wails*, *yodels*, and *tremolos* increased throughout the evening, reached peak activity during the middle of the night (between approximately 22:00 hr to 03:00 hr), and then decreased to lower levels by sunrise (Figs. 3a-3c). Although the output of *hoots* was highest at 20:00 hr and then trailed off to lower levels throughout the night (Fig. 3d), diel variation in output of *hoots* was not statistically significant (Fig. 3d; $F_{1,6706} = 0.1$, $P = 0.74$). During the recording period, 25 April to 28 May, time of sunrise varied from 06:00 to 05:22 hr and time of sunset varied from 20:02 to 20:40 hr.

Loons called significantly more at night than during the day. Based on the average number of calls per night throughout the recording period, each territorial pair of loons produced 166.8 ± 28.1 *wails* per night compared to 9.3 ± 28.1 *wails* during the day (paired t-test; $t_9 = 5.6$, $P = 0.0003$); they produced 36.5 ± 5.2 *yodels* per night compared to 4.8 ± 5.2 *yodels* per day ($t_9 = 6.1$, $P = 0.0002$); and they produced 310.1 ± 39.8 *tremolos* per night compared to 49.4 ± 39.8 *tremolos* per day ($t_9 = 6.5$, $P = 0.001$). In contrast, loons only showed a non-significant tendency to produce more *hoots* at night; loons produced 3.0 ± 1.4 *hoots* per night compared to 0.2 ± 1.4 *hoots* per day ($t_9 = 2.0$, $P = 0.08$). In contrast to the other vocalizations, the reported number of *hoots* is an underestimate of the

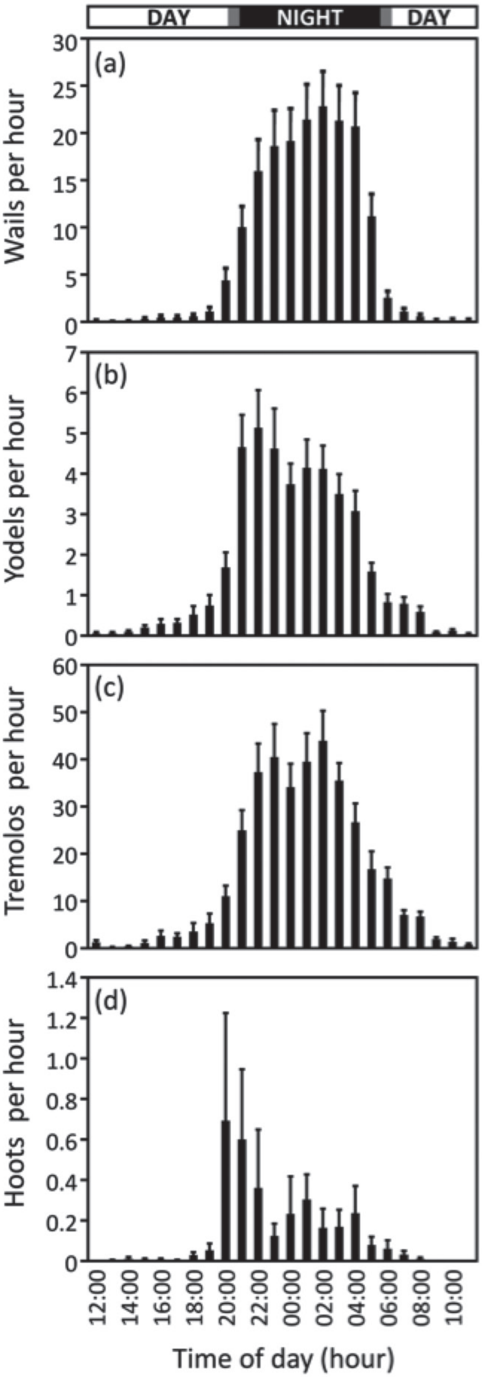

Figure 3. Variation in Common Loon vocal output by time of day. Calling activity is shown as total output per hour for four types of call: (a) *wail* calls, (b) *yodel* calls, (c) *tremolo* calls, and (d) *hoot* calls. Sunset times varied from 20:02 to 20:40 hr and sunrise times varied from 06:00 to 05:22 hr during the recording period (25 April to 28 May); the bar at the top indicates nighttime hours, in black, and the variation in sunset and sunrise times, in gray. Means and standard errors are shown.

total number actually produced by the loons; field observations confirmed that this quiet vocalization was only recorded when loons were close to the autonomous recorders.

Variation in Vocal Output with Time of Year

Loons showed significant variation in vocal output for three of their four vocalizations over the recording period from late April to late May (Fig. 4). Loons showed significant seasonal variation in *wails* (Fig. 4a; Julian day fixed factor in the linear mixed model: $F_{1,6706} = 74.9$, $P < 0.001$), *yodels* (Fig. 4b; $F_{1,6706} = 31.3$, $P < 0.001$), and *tremolos* (Fig. 4c; $F_{1,6706} = 38.9$, $P < 0.001$). Loons produced *hoots* at equivalent levels throughout the recording period (Fig. 4d; $F_{1,6706} = 0.2$, $P = 0.67$). Note that one pair showed unusually high *hoot* output on Julian day 143; when this data point was excluded from the analysis, the same pattern held true: $F_{1,6705} = 2.7$, $P = 0.10$. Output of *wails*, *yodels*, and *tremolos* decreased as the breeding season progressed, whereas output of *hoots* was relatively constant (Fig. 4). The specific timing of clutch initiation of the recorded birds is unknown. Loons are known to commence egg laying in mid- to late May in Ontario (Evers *et al.* 2010), and observations of nest building by the 10 recorded pairs fit this pattern.

The interaction term in the linear mixed model (interaction between Julian day and hour) was not significant for three types of vocalizations: *yodels* (interaction term between day and hour; $F_{1,6706} = 1.4$, $P = 0.24$), *tremolos*

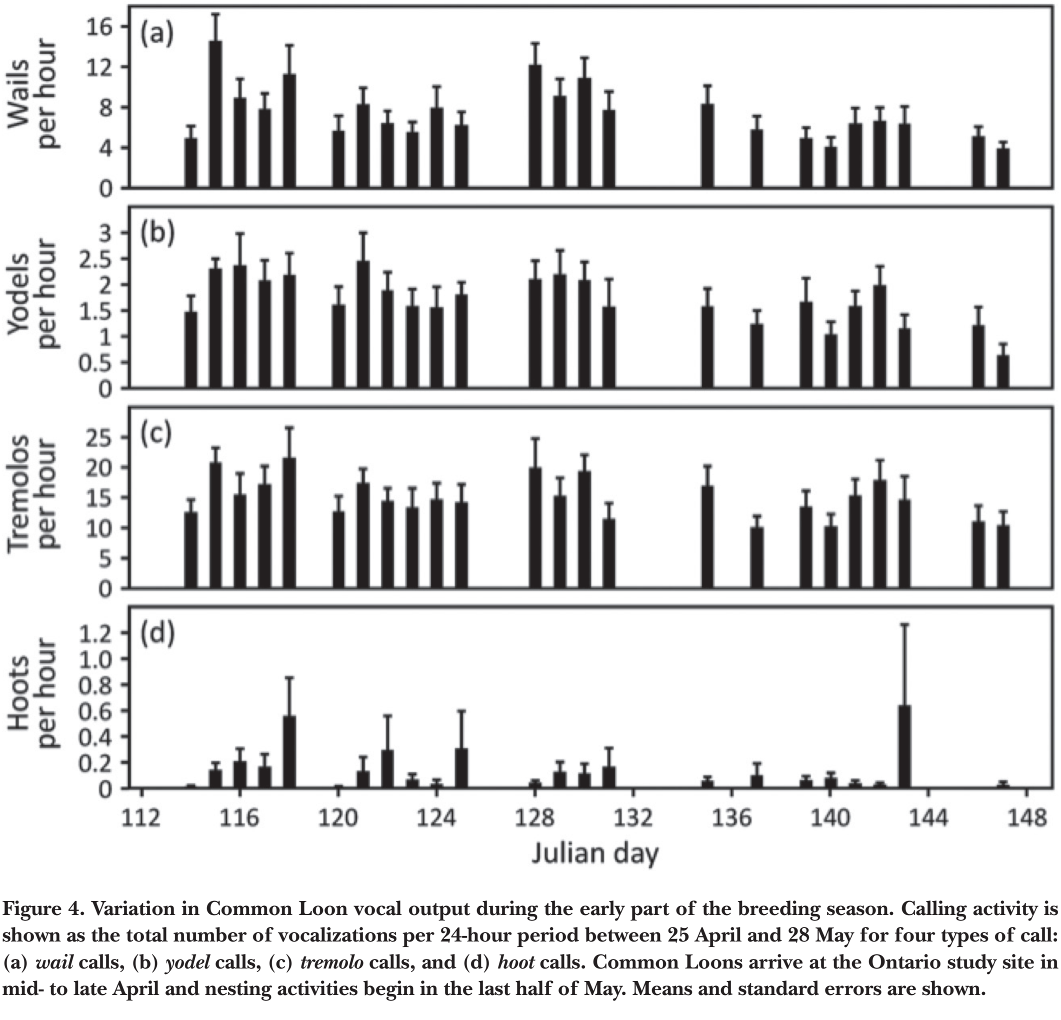

Figure 4. Variation in Common Loon vocal output during the early part of the breeding season. Calling activity is shown as the total number of vocalizations per 24-hour period between 25 April and 28 May for four types of call: (a) *wail* calls, (b) *yodel* calls, (c) *tremolo* calls, and (d) *hoot* calls. Common Loons arrive at the Ontario study site in mid- to late April and nesting activities begin in the last half of May. Means and standard errors are shown.

($F_{1,6706} = 0.8$, $P = 0.38$), and *hoots* ($F_{1,6706} = 0.4$, $P = 0.56$). The interaction term was significant for *wails* ($F_{1,6706} = 6.0$, $P = 0.014$); *wails* showed a greater decrease for nighttime hours than for daytime hours as the breeding season progressed. There was a significant year effect in these models, with more vocalizations in 2009 vs. 2008 for *wails* ($F_{1,6706} = 17.5$, $P < 0.001$) and *tremolos* ($F_{1,6706} = 29.9$, $P < 0.001$), but there was no year effect for *yodels* ($F_{1,6706} = 0.1$, $P = 0.79$) or *hoots* ($F_{1,6706} = 0.4$, $P = 0.51$).

Variation in Vocal Output with Weather

Loon vocal output varied with weather, based on detailed analysis of the five most vocal hours of the night (22:00 to 03:00 hr). Output of *wails*, *yodels*, and *tremolos* showed significant negative relationships with temperature, rainfall, air pressure, and wind speed (Table 1); loons were more likely to produce these three call types when lake water was cooler, when rainfall was light or absent, when air pressure was lower, and when wind was light or absent. Output of *wails* also showed a significant negative relationship with air temperature (Table 1). Output of *hoots*, in contrast, did not vary with any of the weather variables measured (Table 1). There was a significant year effect in the weather models with more vocalizations in 2009 vs. 2008 for *yodels* ($F_{1,1663} = 22.5$, $P < 0.001$) and *hoots* ($F_{1,1663} = 4.2$, $P = 0.04$), but there was no effect of year for *wails* ($F_{1,1663} = 2.1$, $P = 0.15$) or *tremolos* ($F_{1,1663} = 0.2$, $P = 0.63$) in this analysis of the five most vocal hours of the night.

Signal Transmission

I estimated signal transmission distance by calculating the number of microphones in the linear array that recorded vocalizations produced by loons in each of the 10 focal territories. Based on pair-wise comparisons, loon vocalizations transmitted significantly farther at night vs. during the day (Fig. 5). This pattern was true for all three types of long-distance calls; *wails* transmitted farther at night ($t_9 = 10.57$, $P < 0.001$), *yodels* transmitted farther at night ($t_9 = 9.29$, $P < 0.001$), and *tremolos* transmitted farther at night (paired t-test; $t_9 = 4.04$, $P = 0.003$).

DISCUSSION

Based on recordings collected with a 10 km-long array of microphones, I quantified patterns of diel and seasonal variation in the vocal output of Common Loons during the early breeding season, as well as variation in relation to weather conditions. Loons were more vocal at night than during the day for three long-range vocalizations (*wails*, *yodels*, and *tremolos*), but not significantly so for one short-range vocalization (*hoots*). Vocal output declined significantly over the first month of the breeding season for all three long-range vocalizations. Vocal output also varied with weather, showing an influence of water temperature, air pressure, wind speed, and rain. I estimated transmission properties of loon vocalizations by evaluating the number of

Table 1. Common Loon vocal output for four different types of vocalizations (*wails*, *yodels*, *tremolos*, and *hoots*) compared to six weather variables and the 2 years during which recordings were collected. *F*-statistics and *P*-values from a separate linear mixed model for each of the four vocalization types are shown.

	Type of Vocalization							
	Wail		*Yodel*		*Tremolo*		*Hoot*	
Weather Variable	$F_{1,1663}$	*P*	$F_{1,1663}$	*P*	$F_{1,1663}$	*P*	$F_{1,1663}$	*P*
Air Temperature (°C)	10.7	0.001	1.9	0.17	0.1	0.95	2.3	0.13
Water Temperature (°C)	29.6	0.001	7.6	0.006	24.5	0.001	1.6	0.21
Relative Humidity (%)	0.4	0.55	5.8	0.02	0.3	0.55	0.1	0.94
Rain (mm)	9.9	0.001	5.4	0.02	6.8	0.009	0.4	0.52
Air Pressure (kPa)	4.5	0.04	12.4	0.001	6.0	0.01	0.5	0.49
Wind Speed (m/s)	71.8	0.001	25.3	0.001	27.3	0.001	0.1	0.85
Year (2008 vs. 2009)	4.2	0.15	22.5	0.001	0.2	0.63	4.2	0.04

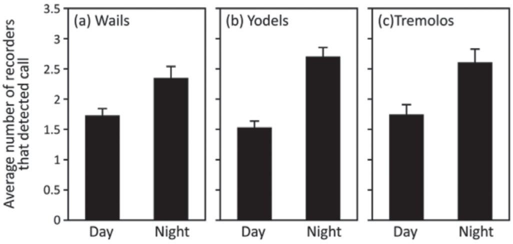

Figure 5. Transmission distance of Common Loon vocalizations during the night vs. during the day. Transmission distance was calculated as the number of microphones that detected a vocalization, moving away from the calling loon in one direction along the linear array. Recorders were positioned approximately 1 km apart. Ten *wail*, *yodel*, and *tremolo* vocalizations were measured from each of the 10 recorded territories from 10 different days and nights. Means and standard errors are shown.

channels in the microphone array that detected vocalizations, and found that all three long-distance loon vocalizations transmit farther at night than during the day. I discuss each of these findings below.

Common Loons showed significantly higher output of *wails*, *yodels*, and *tremolos* at night vs. during the day. Although all three vocalizations were detected at all hours of the day and night, they occurred at high levels between dusk and dawn and at very low levels during daylight hours. It is widely recognized that loons are vocally active at night with observations of their nocturnal vocal behavior dating back many decades (e.g., Olson and Marshall 1952; Rummel and Goetzinger 1975). The current analysis provides quantitative data showing that all three of this species' long-distance signals are significantly more common at night based on long term, round-the-clock recordings. The dissertation research of Wentz (1990) quantified nocturnal variation in vocalizations and showed a peak in nocturnal calling between 3 and 7 hours after sunset, matching the pattern reported here. Wentz (1990) suggested that although call output was similar throughout the night in the early breeding season, loons exhibit a more pronounced peak earlier in the night later in the breeding season.

All three of the long-distance signals of Common Loons play a role in territoriality (Evers *et al.* 2010). Loons may vocalize predominantly at night because of the acoustic advantages of doing so; transmission data reveal that all three of these vocalizations transmit significantly farther at night (explored in detail below), suggesting that nocturnal vocalizations can reach a significantly larger audience of territorial rivals compared to daytime vocalizations. The cost of physical territorial encounters is very high for loons, often resulting in fatalities (Piper *et al.* 2008). By communicating their territorial signals with a broader audience during acoustically advantageous nighttime hours, loons may minimize the high costs of direct encounters.

Although *hoots* were most frequent at night, they were not statistically more likely to occur at night, in contrast to the three long-range calls. In fact, *hoots* were much less common than the other three vocalizations (compare y-axes for Fig. 3). *Hoots* are understood to play a role in maintaining acoustic contact between pair members (Evers *et al.* 2010). The low rates of *hoot* calls I detected in this study may arise for several reasons. As a contact call, *hoots* may not be important during the early part of the breeding season when recordings were collected, because the male and female of a mated pair are often in close proximity at this time of year (D. J. Mennill, pers. obs.). Additionally, *hoots* are a low amplitude signal (Evers *et al.* 2010) and these quiet calls were likely recorded only when loons were near the microphones, whereas the three long-distance vocalizations were detected regardless of the loons' positions on the lakes.

I monitored the vocal behavior of Common Loons during the first month of the breeding period, shortly after birds arrived from migration, through the period of nest building, and into the early egg laying period (Evers *et al.* 2010; La 2010). During this period, loons showed a significant decrease in output of all three of their long-distance signals (*wails*, *yodels*, and *tremolos*). As the breeding season continues, fewer rivals are expected to arrive from migration to compete for territories, and the seasonal decline in territorial call output may reflect the increasingly stable territory dynamics. *Hoots*, which play a role in acoustic contact but have no known territorial function, did not show significant seasonal variation. As a contact call, *hoots* may be expected to increase in frequency during the incubation period when parents are more likely to be physically separated, and during the juvenile period as a contact call between parents and offspring. Extended recording periods, beyond the timing of those I conducted here, will be required to understand how the output of loon vocalizations changes during later breeding periods.

The seasonal pattern I report for Common Loon territorial signals is widespread among birds: high vocal output at early breeding stages followed by a decline as the breeding season continues. This pattern is known across many unrelated taxa, from the calls and sonations of woodpeckers (e.g., Tremain *et al.* 2008) to the songs of many temperate breeding songbirds (e.g., Slagsvold 1977) and the male-female duets of tropical birds (e.g., Topp and Mennill 2008). Variation in Common Loon vocalizations was previously analyzed throughout the breeding season in the dissertation research by Wentz (1990), who did not find significant differences in call output among the pre-breeding, nesting, and post-nesting periods. Her dissertation did not include a detailed night-by-night comparison of the same individuals, as do the data presented here, which clearly reveal a significant decline in output over time.

Common Loons varied their nocturnal vocal behavior with climatic conditions, producing more *wails*, *yodels*, and *hoots* when the water temperature was cooler, when rainfall was light or absent, when air pressure was low, and when wind was light or absent. The negative relationship with water temperature is likely a manifestation of the seasonal decline in vocal output as the breeding season continues; the recordings started just weeks after ice melted from the three study lakes and continued into spring as temperature rose. Only one of the long-range vocalizations, *wails*, showed a negative relationship with air temperature, which may similarly be a relationship coincident with the changing season.

The decrease in vocal output at times of high wind or rain likely represents a signaling strategy by Common Loons. Both rain and wind produce ambient noise that should mask long-distance vocalizations (Ryan and Brenowitz 1985). Moreover, wind may give rise to irregular amplitude fluctuations, which attenuate signals as they transmit from one animal to another (Richards and Wiley 1980). Furthermore, both rain and wind may lead to other changes in loon activities; precipitation, increased wave activity produced by wind, and turbulent air may limit loon swimming and flying behavior, making territorial interactions less common during rainy, windy weather. Low atmospheric pressure is typically associated with rainy and windy weather, yet I found a negative relationship between air pressure and loon vocal activity. Given that loons were less likely to vocalize during periods of wind and rain, the negative relationship with air pressure might indicate increased calling at times before or after the windy, rainy periods when loons are quiet. This relationship requires further investigation.

Quantifying the active signaling space of wild animals is a challenging task, particularly for an animal such as the Common Loon that produces far-carrying vocalizations. By using an array of 10 recorders along a 10-km transect, I estimated loon transmission distances over 10 different nights for each of the three long-distance vocalizations from the 10 focal pairs of loons. Olson and Marshall (1952) previously reported that Common Loon *yodels* can transmit up to 16 km (Evers *et al.* 2010). My estimates suggest that such long-distance transmission is uncommon. In my recordings, *wails*, *yodels*, and *tremolos* were typically detected by sensitive omnidirectional microphones that were located 1 to 3 km away from the vocalizing animal (Fig. 5). The specific position of the vocalizing loons in my study was accurate with a resolution of approximately 1 km, and consequently my measurements have a large degree of error (i.e., approximately 1 km). Yet these measurements suggest that the long-distance vocal signals of loons routinely transmit information several kilometers each direction from the calling animal.

The transmission distances of *wail*, *yodel*, and *tremolo* calls were all significantly higher at night compared to the day, with calls transmitting a kilometer farther at night on average. This represents a significant communication advantage. Based on these transmission data, we may estimate the active signal space of loon long-distance vocalizations. Following the assumption that vocalizations spread spherically from the calling animal, the daytime signal space for *wails*, *yodels*, and *tremolos* is, on average, 7.1 km^2 (i.e., a circle with radius 1.5 km); the same calls produced at night have a signal space of 19.6 km^2 (i.e., a circle with radius 2.5 km). With the average territory size of a pair of loons being 0.7 km^2 (McIntyre 1988), a daytime call might communicate with up to 11 other loon territories; the same call produced at night might communicate with up to 28 other loon territories. Therefore, these recordings show an unambiguous communication advantage for producing long-distance signals at night. This transmission advantage, when considered together with the high costs of physical territorial disputes for Common Loons (Piper *et al.* 2008), may be a strong selective force driving the evolution of nocturnal signaling in this charismatic northern waterbird.

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