

# Dynamics of an Aggressive Vocalization in the Common Loon (*Gavia immer*): A Review

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**Abstract.**—Unlike most waterbirds, Common Loons (*Gavia immer*) have a dynamic vocal repertoire that includes the high-amplitude wail, tremolo, and yodel. This paper is a review of the acoustic structure of the yodel, an aggressive warning signal only given by male Common Loons. The context in which males yodel is described along with the possible adaptive functions of this signal. The yodel is the most acoustically complex vocalization of the Common Loon and contains a wealth of information about the signaler. Suites of frequency and time elements of the yodel appear to communicate information about the identity of the signaler, which may be important for neighbor-stranger, mate, and kin recognition. The peak frequencies of the final note of the introductory phrase and repeat phrases also appear to communicate the condition-dependent fighting ability. Finally, the number of repeat phrases a male adds to its yodel appears to communicate the aggressive motivation, or the willingness a male Common Loon has to escalate a contest. Under various contexts not necessarily unique to Common Loons, these functions may be mutually beneficial to signalers and conspecific and heterospecific receivers, and evoke a number of interesting questions regarding the function of this dynamic signal. Such dynamic vocal signals are rare among waterbirds, and among ornithologists and behaviorists alike elicit questions regarding the conditions that maintain signal honesty among birds communicating fighting ability and aggressive state within the same vocal signal. *Received 20 January 2013, accepted 22 May 2013.*

**Key words.**—aggression, Common Loon, *Gavia immer*, vocal signals, yodel.

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Perhaps nothing more reflects the spirit of the northern wilderness than the calls of the Common Loon (*Gavia immer*). These calls, which inspired the writings of Thoreau (1854) and Leopold (1949), also represent a vocal communication system distinctive from most waterbirds. Advances in the ability to analyze sounds scientifically, as well as reliable methods for marking and distinguishing individual Common Loons in the field (Evers 1993), have greatly enhanced our understanding of the structure and various functions of individual vocalizations of Common Loons. In turn, our better understanding of these vocalizations has provided fascinating and important insight into Common Loon behavioral ecology from the standpoint of both signalers and receivers within various contexts.

The vocal repertoire of the Common Loon is quite large and varied (see reviews by Lindsay 2002 and Evers *et al.* 2010), but three calls are produced loud enough to facilitate long-distance (> 200 m) communication: the wail, the tremolo, and the yodel (Evers *et al.* 2010). Of these, the yodel stands out as the 'song' of the Common Loon in that, following Catch-

pole and Slater (2008), it is given only by a single sex (for Common Loons, only males yodel) during certain situations at specific periods of the year. With so much curiosity among behaviorists, ecologists, and ornithologists regarding the acoustic structure and function of bird song, as well as how evolutionary forces have shaped various aspects of songbird communication and life history (e.g., Wiley and Richards 1982; Catchpole and Slater 2008; Bradbury and Vehrencamp 2011), it is particularly interesting to consider these features in a non-songbird, let alone a non-passerine bird. In this paper, we present an overview of what we have learned about the structure and function of the Common Loon's yodel by describing the acoustic structure of this yodel and the context in which it is given, as well as a review of what information we believe is communicated by the signal. Ultimately, we argue this territorial threat signal exhibits a complexity, in both its structure and adaptive function, atypical of acoustic signals among waterbirds. It reliably communicates a male loon's identity, condition-dependent fighting ability, and aggressive willingness to escalate a contest.

### THE ACOUSTIC STRUCTURE OF THE YODEL

Acoustically, the yodel consists of a single introductory phrase of three to four rising pure tones followed by repeat phrases (Fig. 1). Each repeat phrase consists of two rapid frequency-modulated notes (or 'syllables'); the first syllable is typically shorter, but of similar peak frequency (i.e., frequency of maximum amplitude) to the second syllable as well as to the final note of the introductory phrase (Barklow 1979; Young 1983; Vogel 1995; Mager and Walcott 2007; Mager *et al.* 2007a; Evers *et al.* 2010). These peak frequencies experience minimal acoustic attenuation (McIntyre 1994), which in turn facilitates their long-distance transmission (Mager and Walcott 2007). While each yodel contains a single introductory phrase, a male can vary the number of two-syllable repeat phrases it produces after the introductory phrase. As such, males lengthen yodels not by lengthening individual parameters (as duration parameters exhibit low intra-individual variation; see Barklow 1979; Vogel 1995; Mager and Walcott 2007), but by adding repeat phrases to their yodels (Walcott *et al.* 1999; Mager *et al.* 2007a, 2007b).

### THE CONTEXT OF YODELS

Though male Common Loons yodel on wintering waters prior to migration as well as on migratory staging lakes, they yodel most

frequently on breeding lakes upon their return (Fig. 2), as well as during the nesting period when chicks are about to hatch (Barklow 1979; Young 1983; McIntyre 1988; Mager and Walcott 2007). Males yodel most frequently to conspecifics that either fly over (hereafter referred to as flyovers) or land upon their territories, as well as at heterospecifics intruding within their territories (Mager and Walcott 2007). This includes a number of human intrusions, including boats that enter and airplanes that fly over the territory. Males tend to yodel primarily during the early morning and late evening when territorial flyovers and intrusions are frequent (Young 1983; Wentz 1990; Mager 1995). However, at night males will yodel at vocalizations from conspecifics occupying nearby territories, most notably during nocturnal choruses (Rummel and Goetzinger 1975; Young 1983; Wentz 1988, 1990; La 2010). Males assume one of two physical postures when they yodel: the crouch-posture and the vulture-posture (Rummel and Goetzinger 1975, 1978). In the crouch-posture, a male will remain on the water surface as it lowers its head and stretches its neck horizontally just above the water surface, and either faces the intended recipient (often when the receiver is on the territory) or rotates its body as it remains in its crouch-posture (most often if the receiver is flying over the territory). In the vulture-posture, a male actively paddles its legs so that its body remains vertical and above the water surface,

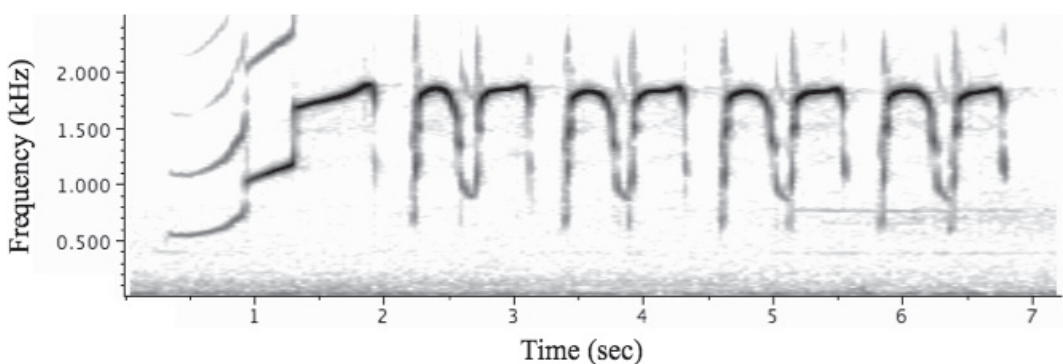


Figure 1. Acoustic spectrogram showing the change in frequency (in kHz) of a typical Common Loon yodel over time (in sec). Structurally, the yodel consists of two fundamental features: an introductory phrase of three to four notes that rise in frequency, and a motif of two-syllable repeat phrases following the introductory phrase.

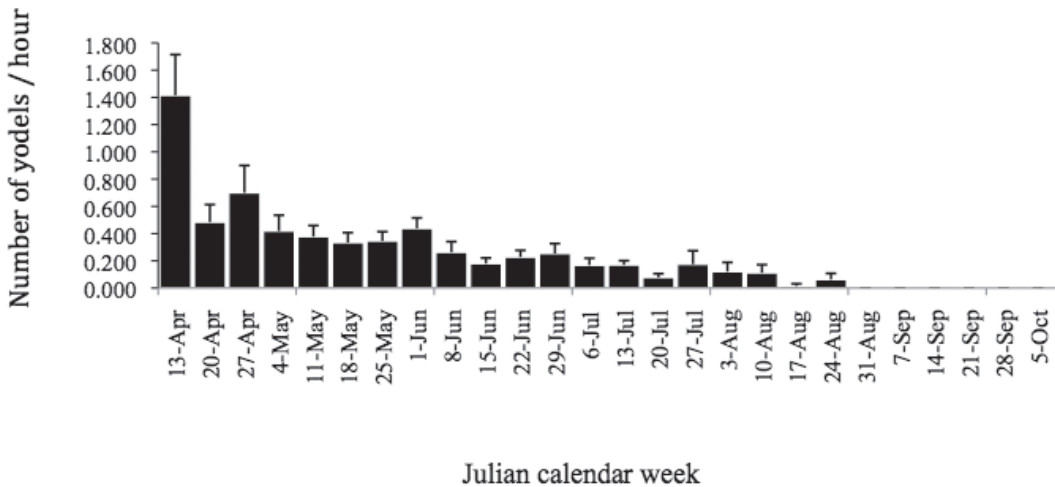


Figure 2. Mean ( $\pm 1$  SE) yodeling rates of 38 males within the same population of Common Loons between 15 April (first day of ice-out) and 31 August, 2001-2007. The incubation period of Common Loons usually begins between late-April and the end of May, and the incubation period usually lasts between 25-28 days (McIntyre 1988). Males yodel significantly more often during the time when males are returning and reestablishing all-purpose territories (rmANOVA  $F_{37,19} = 9.299$ ,  $P < 0.0001$ ).

spreads out its wings, and points its neck and bill horizontally toward the perceived receiver (usually conspecific intruders  $< 20$  m from the signaler; Mager *et al.* 2012) when the probability of contest escalation between individuals is greater. During escalated confrontations, both males may yodel simultaneously at each other in the vulture-posture. As such, the vulture-posture may enhance the information communicated by the yodel (J. F. Barr, as cited by McIntyre 1988), or perhaps signal additional information regarding its fighting ability or aggressive state to the receiver (see Johnstone 1996 and Rowe and Guilford 1999).

Because males yodel frequently in the early breeding season, initial functional hypotheses were associated with mate attraction and/or pair bond reestablishment and maintenance (Sim 1923; Sjølander and Ågren 1972); however, few studies have experimentally substantiated predictions associated with these. Interestingly, males also yodel frequently at a time when chicks are expected to hatch, presumably when it is most critical to seasonal reproductive success (Mager and Walcott 2007). Additionally, in contrast to floaters which do not approach playback yodels, territorial males yodel and quickly approach conspecific and

heterospecific intruders (Fig. 3), as well as territorial neighbors at territorial borders when the probability of aggression following the behavior is high (Rummel and Goetzing 1975; Barklow 1979). This territorial male yodeling and approach behavior occurs even during incubation, as 87% of males ( $n = 15$ ) leave the nest and approach upon hearing a yodel, whereas incubating females (7%,  $n = 14$ ) rarely leave the nest ( $\chi^2$  test of independence  $\chi^2 = 18.340$ ,  $P < 0.0001$ ). As such, the yodel seems

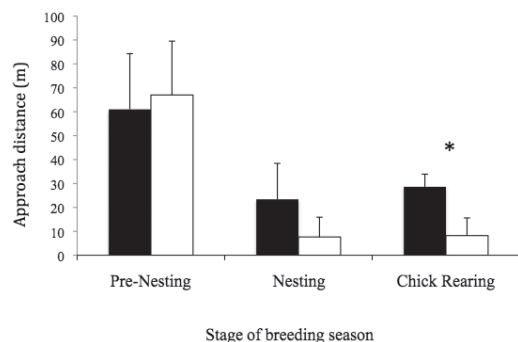


Figure 3. Mean ( $\pm 1$  SE) approach distances of male and female Common Loons within a 1-min period following playback yodels from unfamiliar males during the pre-nesting, nesting, and chick-rearing period. \* indicates  $P < 0.05$ .

to serve more as an aggressive warning or threat signal (e.g., Munro 1945; Rummel and Goetzinger 1975, 1978; Barklow 1979; Young 1983; McIntyre 1988; Wentz 1990; Vogel 1995; Lindsay 2002); however, its function in mate attraction or establishing and maintaining a pair bond should not be discounted until studies explicitly examining predictions from these hypotheses have been conducted.

#### THE YODEL AS A SIGNAL OF INDIVIDUAL (OR CLASS) IDENTITY

Many avian signals facilitate the recognition of sex (e.g., Taoka *et al.* 1989; Nuechterlein and Buitron 1992), mates (e.g., White and White 1970), kin (e.g., Beecher 1988, 1991; Jouventin *et al.* 1999; Aubin and Jouventin 2002; Draganoiu *et al.* 2006), and territorial neighbors (Wiley *et al.* 1991; Ydenberg *et al.* 1988; Lambrechts and Dhondt 1994; Tibbetts and Dale 2007). Because only males yodel, it is reasonable to assume that the yodel permits sexual recognition by conspecifics within this monomorphic species (males and females are similar in plumage, but males tend to be larger than females; Evers *et al.* 2010). The idea that the yodel communicates the individual loon's identity for additional functional benefits arose from initial recognition of individually identifiable acoustic signatures within sonograms of recorded yodels (Barklow 1979; McIntyre 1988; Miller 1988; Miller and Dring 1988). Vogel (1995) used stepwise discriminant function analyses to identify four duration, two latency, and one absolute frequency parameters that distinguished individual males. More comprehensive multivariate discriminant analyses have identified suites of frequency, latency, and duration parameters of the introductory phrase (Walcott *et al.* 1999; Walcott and Evers 2000; Lindsay 2002) and of the repeat phrases (Lindsay 2002) that collectively are individual-specific.

The individual recognition hypothesis was strengthened by acoustic playback experiments that revealed one of the functions of this recognition is neighbor/stranger discrimination. Though Lindsay (2002) found that residents responded more aggressively

to unfamiliar yodels regardless of the peak frequencies of the yodel, Mager *et al.* (2010) found that territorial pairs responded more aggressively and with greater alarm to yodels from unfamiliar individuals that were of lower peak frequency than the resident male's yodel. Because males with greater condition-dependent fighting abilities produce lower peak-frequency yodels (see below), this demonstrated a level of neighbor/stranger discrimination in which individual responses are associated with the perceived threat. Playback studies have also revealed that elements found within the introductory phrase, rather than those within the repeat syllables, may be more important for neighbor/stranger discrimination (Mager *et al.* 2010).

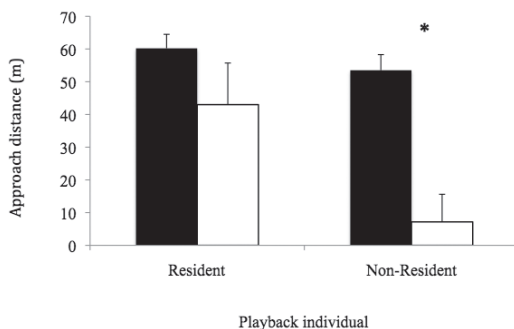
In a social system whereby loons of either sex frequently challenge and usurp each other from breeding territories (Piper *et al.* 2000), Walcott *et al.* (2006) found that males will change individually distinctive elements of their yodels when they move to different territories. This change not only leads to a yodel that is significantly different from its previous yodel (as males do not change yodels during their tenure on their previous territories), but also it is significantly different from the yodels of previous territorial residents (Walcott *et al.* 2006). This demonstrates that males are familiar not only with the acoustic structure of their own yodels, but also the structure of the yodels of other neighboring males.

Empirical support of the hypothesis that the yodel facilitates individual recognition for neighbor/stranger discrimination does not discount the possibility that the yodel facilitates discrimination in other contexts, including mate/non-mate and kin/non-kin discrimination. For example, preliminary data from a small sample of individuals ( $n_{\text{males}} = 11$ ,  $n_{\text{females}} = 10$ ) indicate solitary females (females residing on their territories when males are not on the territory) do not approach yodels of unfamiliar males as closely as solitary females responding to playback yodels of their partners (Wilcoxon  $Z = 2.025$ ,  $P = 0.043$ ), nor as closely as solitary males responding to unfamiliar yodels (Wilcoxon  $Z =$

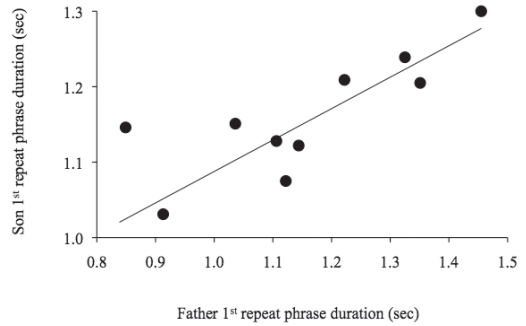
0.013,  $P = 0.010$ ; Fig. 4), possibly indicating a level of mate recognition that would permit discrimination of approaching unknown individuals. Additionally, elements within repeat phrases may be similar between fathers and sons (see Fig. 5) at a level to facilitate kin recognition. This communication would be adaptive for territorial selection and defense strategies adopted by local populations where individuals are long-lived (McIntyre 1988; Evers *et al.* 2010), where young return to their natal area (e.g., Piper *et al.* 2012), and where individuals frequently interact with kin (e.g., Piper *et al.* 2001). These findings warrant further examination of predictions associated with these possible adaptive functions of individual or class recognition through the yodel.

#### THE YODEL AS A SIGNAL OF FIGHTING ABILITY

Many acoustic signals convey strength, condition, or other qualities that are directly related to an individual's probability of winning a contest (Parker 1974; Archer 1988; Catchpole and Slater 2008). The communication of condition-dependent fighting ability would appear to be extremely important among Common Loons, where territorial intrusions are frequent and sometimes lead to severe, if not lethal, confrontations (Piper *et al.* 2000, 2008; Mager *et al.* 2008, 2012). Indeed,



**Figure 4.** Mean ( $\pm 1$  SE) approach distances of solitary male (dark bars) and female (open bars) Common Loons within a 1-min period following playback yodels from resident and unfamiliar males, regardless of stage of breeding season. Sample sizes are indicated below each bar. \* indicates  $P < 0.05$ .



**Figure 5.** Correlation between the duration of the first repeat phrase of yodels of fathers and sons ( $n = 10$  father/son pairs, slope = 0.328, coefficient of correlation  $r = 0.629$ ,  $P = 0.006$ ). This, in turn, may indicate similarities in the repeat phrases of the yodel that may facilitate recognition of related males.

the yodel also communicates information about male body size, which in turn reflects his condition-dependent fighting ability, through the peak frequencies of his yodels. Like many animals (see reviews by Archer 1988; Riechert 1998; and Bradbury and Vehrencamp 2011), including birds (e.g., Searcy 1979), heavier loons acquire higher quality territories (Evers 2001) and experience longer tenures on breeding territories (Piper *et al.* 2000). As such, variation in signal elements that corresponds with variation in body mass may allow these elements to serve as reliable indicators of fighting ability (Endler 1993; Bradbury and Vehrencamp 2011). For many species, including birds (e.g., Tubaro and Mahler 1998; ten Cate *et al.* 2002; Martin *et al.* 2011; Linhart *et al.* 2012; and reviews by Wällschlager 1980 and Ryan and Brenowitz 1985), larger individuals produce lower-frequency vocalizations. Across both macrogeographic (McIntyre 1988; Mager *et al.* 2007a) and microgeographic (Mager *et al.* 2007b) scales, larger male Common Loons produce yodels that are of lower peak frequencies. Not only are these relationships between body size and condition strong, but acoustic playback results indicate territorial pairs recognize these differences, as they are more alert to and responded more aggressively to broadcast yodels manipulated to be lower in peak frequencies

(Mager *et al.* 2007b). Additionally, as males lose or gain weight over their tenures on their territories (males tend to lose weight during their mean 5-year tenures on territories in north-central Wisconsin; Piper *et al.* 2008), they experience corresponding changes in the peak frequencies of their yodels (Mager *et al.* 2007b). Together, the strong relationship between loon body size and yodel peak frequencies, the association of body size with male fighting ability, and the results of acoustic playback studies have led us to infer that loons can assess conspecific condition-dependent fighting abilities by considering the peak frequencies of their yodels.

As a reliable signal of condition-dependent fighting ability, honesty may not be maintained by receiver-dependent factors (i.e., those that make the signaler vulnerable to attack, or receiver retaliation of dishonest signaling; see Vehrencamp 2000). For example, loons that yodel at frequencies lower than those predicted by the relationship between body size and peak frequency do not experience greater contest escalation (slope of general linear model regression of proportion of contests that escalate into physical fights against residual yodel peak frequency = 0.500,  $r^2 = 0.014$ ,  $n = 50$ ,  $P = 0.42$ ), which might indicate a cost in dishonest signaling. Possibly, as a non-passerine bird possessing a tracheobronchial syrinx (J. N. Mager and M. Pokras, pers. obs.), constraints associated with the physical or physiological ability of males to produce high-amplitude sounds at low frequencies may be more responsible. As recently noted by Linhart *et al.* (2012), many non-passerines may lack the ability to produce vocalizations with wide facultative bandwidths (Gaunt 1983), which may prevent smaller males from producing low-frequency yodels loud enough to be transmitted across great distances. As such, in this context the yodel may be either a quality handicap or quality index signal of male fighting ability whereby honesty is maintained by costs or physical constraints associated with low-frequency sound production (see reviews by Vehrencamp 2000 and Bradbury and Vehrencamp 2011). These

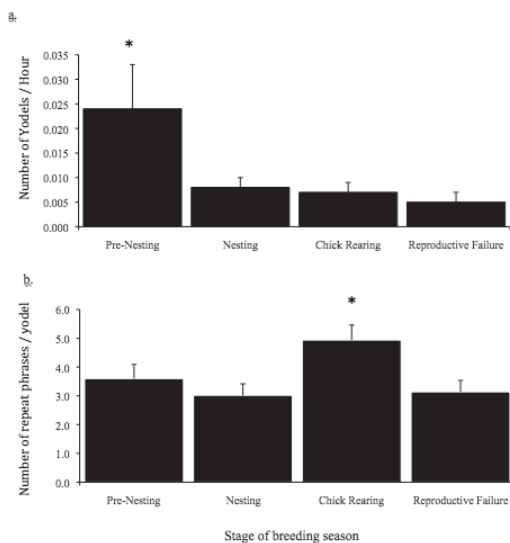
factors responsible for maintaining signal honesty are still quite speculative, however, and need to be considered further.

As a consequence of signaling fighting ability through peak frequencies of the yodel, one could imagine that males that produce high-frequency yodels would be reluctant to reveal poorer fighting abilities. This does not appear to happen, however, as males that produce higher peak frequencies yodel just as frequently as males that produce lower peak frequencies (slope of general linear model regression of yodeling rate against peak frequencies of male yodels = -0.681,  $r^2 = 0.012$ ,  $n = 50$ ,  $P = 0.45$ ). Rather, lighter males produce yodels with more repeat phrases (Mager *et al.* 2008). In consideration of the long-held belief that the number of repeat phrases directly communicates the level at which a male is willing to attack, if necessary, males of smaller body size (and hence poorer fighting ability) may compensate for signaling poorer condition fighting ability by signaling a greater willingness to escalate a contest.

#### THE YODEL AS A SIGNAL OF WILLINGNESS TO ESCALATE A CONTEST

An individual's ability to hold onto a particular resource is not only related to its fighting ability, but also its willingness to escalate a contest. This willingness to escalate often is referred to as an individual's aggressive motivation, and signals that are graded to reflect greater aggressive motivation are characterized by changes in the signal with increasing aggressive motivational state that are also associated with a greater probability of aggressive escalation by the signaler and elicit different behavioral responses by receivers (Searcy and Beecher 2009). In support of the first condition, studies have found that males yodel more frequently when they are establishing or reestablishing territories (Figs. 2 and 6a) and when chicks are about to hatch (e.g., Barklow 1979; McIntyre 1988; Mager and Walcott 2007), both situations arguably when territories are most valuable for seasonal reproductive success.

However, male loons do not yodel more frequently to intruding males during stages of contest escalation that are more prone to lead to physical confrontation. Rather, they produce yodels with more repeat phrases and are more likely to assume the vulture-posture when yodeling (Barklow 1979; Mager *et al.* 2012). Additionally, males give yodels with more repeat phrases to similar stimuli during the chick rearing period (Fig. 6b) as well as when territory quality is enhanced by the addition of nesting platforms, indicating a direct relationship between resource value and the willingness of a male to defend it from conspecifics (Mager *et al.* 2008). Results of playback studies have demonstrated that territorial pairs respond with greater alarm and aggression to playback yodels from unfamiliar males having more repeat syllables (Mager *et al.* 2012). These findings support Barklow's (1979) contention that, as an aggressive signal, the yodel is a signal that males lengthen by adding repeat phrases to communicate greater aggression.



**Figure 6a.** Mean ( $\pm 1$  SE) yodeling rates of 20 male Common Loons within the north-central Wisconsin population during 2004-2007. \* indicates  $P < 0.05$ .

**Figure 6b.** Mean ( $\pm 1$  SE) number of repeat phrases given per yodel of five males within the population in which yodeling to conspecifics was observed during productive (chicks fledged) and unproductive years during 2004-2007. \* indicates  $P < 0.05$

## DISCUSSION

The Common Loon's acoustic communication system is not only atypical of most waterbirds, but also exhibits a complexity that is similar to that of many songbirds. Within the loon's repertoire of long-distance acoustic signals, the male yodel is particularly complex and rich in information. Currently, rather than a mate attraction signal, the yodel has been studied as a sophisticated threat signal given during aggressive intrasexual contests. Observational and experimental studies indicate that the yodel communicates an individual male's identity (through suites of time and frequency parameters) that is important not only for neighbor/stranger discrimination, but also possibly for mate and kin recognition. Additionally, males appear to communicate condition-dependent fighting ability through the peak frequencies of the final note of the introduction and the two-syllable repeat phrases, and willingness to escalate a contest through the number of repeat phrases a male produces within its yodel. Preliminary data indicate that honest communication of these elements is associated with production costs associated with quality handicap or quality index signals, and further studies that consider these costs would be most intriguing. Vocalizations that communicate both individual fighting ability and motivation through different parameters, and specifically through the peak frequencies and the length of the vocalization respectively, within the same signal has been noted more frequently among birds (see discussion by Linhart *et al.* 2012), and this communication system may serve as a model for adaptive strategies of communicating both fighting ability and aggressive state within a single vocal signal among birds, let alone among waterbirds.

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