Male common loons, *Gavia immer*, communicate body mass and condition through dominant frequencies of territorial yodels

JOHN N. MAGER III*, CHARLES WALCOTT* & WALTER H. PIPER†

*Department of Neurobiology and Behavior, Cornell University
†Department of Biological Sciences, Chapman University

We investigated whether male-specific territorial 'yodels' communicate information about individual size and condition in the common loon. Individuals in better condition and of larger body mass, but not larger structural body size, produced lower-frequency yodels, and changes in dominant frequencies of yodels between years reflected changes in male body mass and condition. An acoustic playback experiment indicated that potential receivers vocalized sooner and more often in response to low-frequency yodels, a possible indication that dominant frequencies of the yodel may communicate condition-dependent fighting abilities. Physiological constraints associated with mass and/or condition may preserve honest signalling by preventing small individuals from producing low-frequency yodels.

Keywords: body size; common loon; *Gavia immer*; honest signalling; territoriality; vocal communication

Territorial signals have evolved to communicate reliable information about a signaller's identity, location, fighting ability and motivational state (Bradbury & Vehrencamp 1998). While signal elements that communicate motivation are often linked to the value of a territory, signal elements that communicate a signaller's fighting ability are often related to physical and/or physiological qualities, such as body size and/or condition, that are correlated with the probability of contest victory (Bradbury & Vehrencamp 1998).

Several species of animals communicate fighting ability through the dominant frequencies of acoustic signals (Davies & Halliday 1978; Clutton-Brock & Albon 1979; Wagner 1989). However, few studies have used playback

Correspondence and present address: J. N. Mager, III, Department of Biological and Allied Health Sciences, Ohio Northern University, Ada, OH 45810, U.S.A. (email: j-mager@onu.edu). C. Walcott is at the Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A. W. H. Piper is at the Department of Biological Sciences, Chapman University, One University Drive, Orange, CA 92866, U.S.A.

to investigate this possibility among birds, despite correlations between body size and the dominant frequency both within species (Bretagnolle 1989; Genevois & Bretagnolle 1994; Podos 2001) and across species (Wallschläger 1980; Tubaro & Mahler 1998; Bertelli & Tubaro 2002). Specifically, no studies have tested the hypothesis that birds signal fighting ability through the dominant frequencies of their vocalizations by examining the prediction that receivers should respond differently to signals of different dominant frequency. The lack of research in this area is surprising, because the dominant frequencies of vocalizations in nonsongbird species may be important for communicating male quality and/or condition in the context of both male–male competition (e.g. Furlow et al. 1998) and female attraction (e.g. Beani & Dessì-Fulgheri 1995; Appleby & Redpath 1997; Miyazaki & Waas 2003).

The yodel (Fig. 1) is a vocalization given by male common loons in response to territorial intrusions. Research has suggested that the yodel communicates a male's identity (Walcott et al. 1999; Lindsay 2002) and motivational state (Barklow 1979a; McIntyre 1988). The dominant
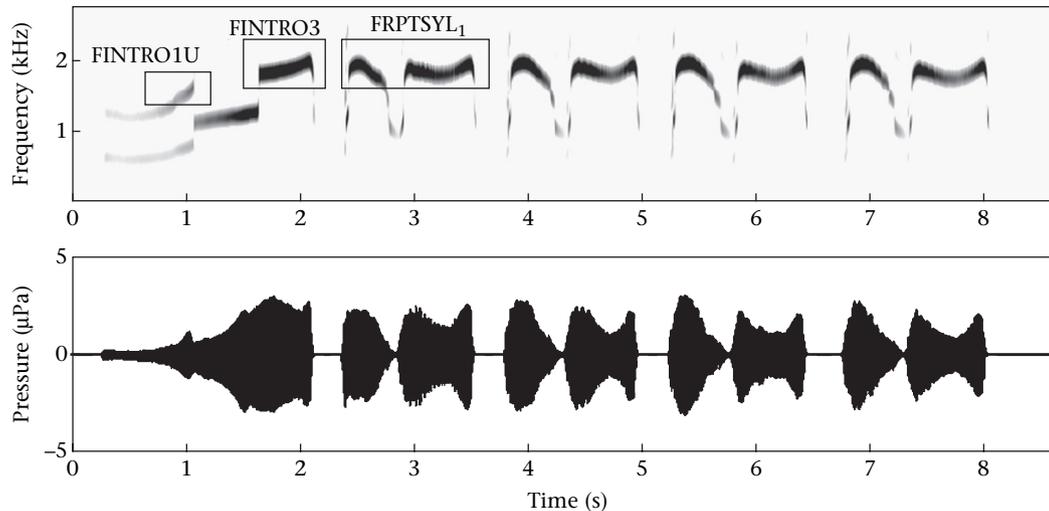
Figure 1. Sound spectrogram (above) and waveform (below) of a typical yodel. Yodels consist of an introductory phrase of three to four notes, followed by a strophe of two-syllable repeat phrases. $FINTRO1U_w$: the frequency of the end of the second harmonic of the first note of the introductory phrase; FINTRO3: the dominant frequency of the final note of the introductory phrase; $FRPT_1$: the dominant frequency of the first repeat phrase; FALLRPT: the dominant frequency of the entire series of repeat phrases.

frequencies of yodels may be ideal for communicating fighting ability over distances, because (1) they fall within a range that experiences little attenuation (Wiley & Richards 1982; McIntyre 1994), (2) they vary little within but greatly between individuals (Barklow 1979a; Walcott et al. 1999) and (3) they show a direct correlation with body mass between populations (McIntyre 1988).

We examined the possibility that male loons communicate fighting ability through the yodel. Specifically, we investigated whether relationships exist between structural body size, mass and dominant yodel frequency within a population, and whether receivers respond differently to yodels that vary in their dominant frequencies.

METHODS

Study Area and Species

We conducted this study during 2001−2004 on roughly 100 lakes in Oneida County, Wisconsin, U.S.A. (45°42′N, 089°37′W). Most loons within this area have been marked with unique combinations of coloured leg bands (Evers 1993) to facilitate reliable identification of individuals in the field.

Common loons are genetically monogamous (Piper et al. 1997), show high territory and mate fidelity (Piper et al. 2000), and aggressively defend all-purpose breeding territories from conspecifics (McIntyre & Barr 1997). Breeding pairs return to lakes of our study area after ice-out, in mid-April. Females lay two eggs, both parents share in incubating duties for 28 days, and semiprecocial chicks are fed and protected by both parents until fledging, at 8−10 weeks (McIntyre & Barr 1997; Mager 2000). Territorial intrusions are frequent during the breeding season; many represent prospecting by prebreeders (Piper et al. 2006). At times, intrusions result in aggressive interactions

and culminate in displacement (Paruk 1999; Piper et al. 2000). Forty-one per cent of all territory acquisitions by loons in northern Wisconsin occur through territorial take-over (Piper et al. 2000).

Protocol for Eliciting and Recording Yodels

We recorded at least 10 yodels from each male each year in response to playback of recordings of flight tremolos and yodels to males on their territories. Playbacks entailed broadcast of vocalizations through a RadioShack Power-Horn speaker at about 70−80 dB when a male was within 100 m of the speaker. We recorded a few yodels that occurred in response to intruders during behavioural observations. We recorded yodels with a Sennheiser MKH-70 shotgun microphone connected to a HHB PortaDAT recorder and converted them into AIFF sound files using the Canary sound analysis package (v. 1.5, Cornell University Bioacoustics Research Program, Ithaca, New York, U.S.A.).

We used a fast Fourier transformation (using a 349.7-Hz bandwidth, 4096 points per frame, 50% overlap of frames in successive transforms, and a Hamming sampling window) to generate sound spectrograms, and we identified four frequency parameters with low coefficients of intraindividual variation (Barklow 1979a; Vogel 1995). We then used Canary's 'peak frequency' measurement to determine dominant frequency (that at which the amplitude was highest) for each parameter. The four measured components were: (1) $FINTRO1U_w$, the end of the second harmonic of the first note of the introductory phrase, (2) FINTRO3, the final note of the introductory phrase, (3) $FRPTSYL_1$, the first repeat phrase and (4) FALLRPTS, the entire series of repeat phrases (including $FRPTSYL_1$; Fig. 1). $FINTRO1U_w$, FINTRO3 and $FRPTSYL_1$ were correlated, so we derived a principal component (PC) from that correlation that had an eigenvalue of 1.936 and explained 62.6% of total variation.

Assessment of Male Body Size and Condition

We captured loons at night by spotlighting (Evers 1993) to assess each male's structural body size and nutrient reserve mass, as defined by Piersma & Davidson (1991). We measured tarsus length (tarsal joint to the insertion of the first digit), unflattened wing chord (carpal joint to tip of the outermost primary), bill length (maxilla length from anterior tip to posterior dorsal edge), bill width (lateral bill length at the nares) and bill height (dorsoventral length at the nares) as indicators of structural body size. Tarsus length was correlated with all other measures (Pearson correlation: $r_{51} = 0.351 - 0.407$, all $P < 0.05$); thus, we derived a 'body size index' (BSI) from the first PC score generated from these five body size measures (eigenvalue = 2.398, explaining 48% of variation), such that higher index scores indicated larger body size. We calculated body condition from residual scores of an ordinary least squares (OLS) regression of individual body mass against BSI, and assumed that individuals with higher scores were in better condition (Brown 1996; Schulte-Hostedde et al. 2005). We investigated whether frequency components of yodels covaried with structural body, body mass and body condition by calculating Pearson correlation coefficients and linear regression coefficients (r^2). We used the sequential Bonferroni method (Rice 1989) to determine statistical significance of our 40 multiple correlation analyses, but we report all correlations for which P values were below 0.05 to avoid being too conservative (Moran 2003).

Playback Experiment

To determine whether breeding pairs responded to yodels with low dominant frequencies, we conducted an acoustic playback experiment at the edge of a territory during 2130−0230 hours, when loons are vocal (Wentz 1990). At a specific time (±20 min) and in random sequence on three successive nights, we played to each pair one of three versions of a yodel from an unfamiliar male (> 8 km distant) that contained three repeat syllables. The first version was unmanipulated; the second was artificially increased in frequency by 200 Hz (using Digital Audio Editor software, v. 4.0, GoldWave, Inc. 2002, St John's, Newfoundland); the third was artificially decreased in frequency by 200 Hz. To prevent pseudoreplication, we used a unique set of three yodel versions for each territory (Kroodsma et al. 2001). Following Lindsay's (2002) protocol, we broadcast one yodel from a compact-disc player connected through a RadioShack 20-W amplifier and Super PowerHorn speaker at roughly 80 dB (∼3 m from the speaker), waited 5 min, then repeated the broadcast and wait periods twice more. We quantified pairs' vocal responses during the 15-min period between the first playback and 5 min after the third and final playback. We measured (1) latency between playback and first vocal response and (2) number of tremolo, wail and yodel responses by the pair. Wails are the characteristic mournful 'cries' of the common loon that structurally consist of one, or a series, of pure tones that often vary in duration.

They are believed to function primarily as a contact call between pair members or between parents and chicks (Barklow 1988; McIntyre 1988). Tremolos are frequency-modulated tones with superimposed modulations of amplitude that are often referred to as the 'laughs' of the common loon. Tremolos have been primarily regarded as alarm calls, and often are given when there is conflict to approach or flee from territorial disturbances (Olson & Marshall 1952; Sjölander & Årgen 1972; Barklow 1979a, b; McIntyre 1988). Adults give tremolos (often antiphonally) when disturbed, particularly when caring for young, so it is believed that tremolos are also defensive or agonistic calls (Barklow 1979a, b; McIntyre 1988). We used a Friedman's ANOVA to look for differences in these vocal responses to the three different classes of yodel. We also used the PROC MIXED procedure (SAS Institute Cary, North Carolina, U.S.A.; Singer 1998; Johnson 2002) to construct a linear growth model to determine whether there were significant changes in the vocal responses of pairs to increasing dominant frequency as represented by each playback group. Unless noted otherwise, we used a significance level of 0.05.

RESULTS

Males varied considerably in mass, structural body size and dominant frequency of the yodel (Table 1). We found weak correlations between external measures of loon structural body size and dominant frequencies of the yodel that were nonsignificant by the sequential Bonferroni correction: wing chord was negatively correlated with dominant frequency of the first repeat phrase (FRPTSYL₁; $P = 0.038$) and the entire motif of repeat phrases (FALLRPT; $P = 0.028$; Table 2); mean tarsus length was positively correlated with FINTRO1U ($P = 0.048$; Table 2). Some of the measurements of dominant frequency, however, were significantly related to both body mass and condition (Table 2, Fig. 2). In particular, the first principal component derived from the dominant

Table 1. Means and ranges of male body size and yodel frequency measurements recorded from individual male common loons caught in Oneida County, Wisconsin, between 2001 and 2004

Measurement	N	Mean±SE	Range
Body measurement			
Body mass (g)	55	4530±36	3900−4982
Bill length (mm)	53	88.70±0.53	80.25−95.40
Bill width (mm)	53	17.80±0.37	12.00−23.35
Bill height (mm)	53	27.15±0.28	19.65−31.85
Mean tarsus length (cm)	52	6.40±0.06	5.65−7.65
Mean wing chord (cm)	52	37.75±0.14	36.05−40.25
Yodel frequency parameter*			
FINTRO1U$_w$ (kHz)	55	1.478±0.007	1.350−1.591
FINTRO3 (kHz)	55	1.809±0.009	1.607−1.966
FRPTSYL₁ (kHz)	55	1.794±0.017	1.278−2.058
FALLRPT (kHz)	55	1.797±0.015	1.323−1.973

*See text.

Table 2. Pearson correlation coefficients (r) between body size measurements and frequency parameters of yodels from male common loons caught between 2001 and 2004

Measurement	N	FINTRO1U$_W$	FINTRO3	FRPTSYL$_1$	FALLRPT	FPC1†
Wing chord	52	0.090	−0.140	−0.288	−0.304	−0.146
Bill length	53	0.002	−0.195	−0.147	−0.063	−0.212
Bill width	53	0.171	−0.024	0.005	−0.082	0.094
Bill height	53	0.219	−0.027	−0.179	0.020	−0.013
Tarsus length	52	0.276	0.115	−0.051	0.024	0.149
Body size index‡	52	0.091	−0.064	−0.059	0.032	−0.054
Body mass§	55	−0.460*	−0.585**	−0.315	−0.266	−0.639**
Body condition††	52	−0.417*	−0.530**	−0.309	−0.252	−0.583**

*Significant at a sequential Bonferroni-corrected α of 0.05; **Significant at a sequential Bonferroni-corrected α of 0.01.
†Principal component generated from FINTRO1U$_w$, FINTRO3 and FRPTSYL$_1$.
‡First principal component generated from five linear measures of body size.
§Correlations between log-transformed values.
††Measured from OLS residuals of correlation between body mass and body size index.

frequency measures was strongly related to both body mass ($r^2 = 0.399$, $N = 53$, $P < 0.0001$) and condition ($r^2 = 0.340$, $N = 51$, $P < 0.0001$). Correlations between body mass and FRPYSYL$_1$ ($P = 0.0157$), between body mass and FALLRPT ($P = 0.0452$) and between body condition and FRPTSYL$_1$ ($P = 0.0252$) were nonsignificant by the sequential Bonferroni correction (Table 2).

Absolute mass and condition were not the only factors correlated with yodel frequency; change in mass was indicated by change in frequency. Males that gained mass between years within the period 2001−2005 produced lower-frequency yodels, while those that lost mass produced higher-frequency yodels (Fig. 3). A similar relationship was found between changes in dominant frequencies and changes in body condition: loons of enhanced condition tended to produce lower-frequency yodels (slope of regression = −0.355, $r^2 = 0.556$, $N = 14$ males, $P = 0.002$).

Low-frequency yodels, which indicated large body mass and enhanced condition, elicited greater responses during playbacks. Breeding pairs responded sooner and produced more wails, and males yodelled more following playback of low-frequency yodels (Table 3). In addition, the latency before pairs responded vocally (Friedman ANOVA: $F_{1,41} = 14.30$, $P = 0.0005$), the number of wails given by subjects ($F_{1,41} = 4.58$, $P = 0.038$) and the number of yodels given by males ($F_{1,41} = 7.09$, $P = 0.011$) could be attributed to the decreasing dominant frequency (FINTRO3) of the playback yodel.

DISCUSSION

How Does the Yodel Function in the Assessment Strategies of Male Loons?

A male's fitness depends not only upon the quality of a territory he acquires but also upon his ability to obtain a territory in the first place. Therefore, a prebreeder should
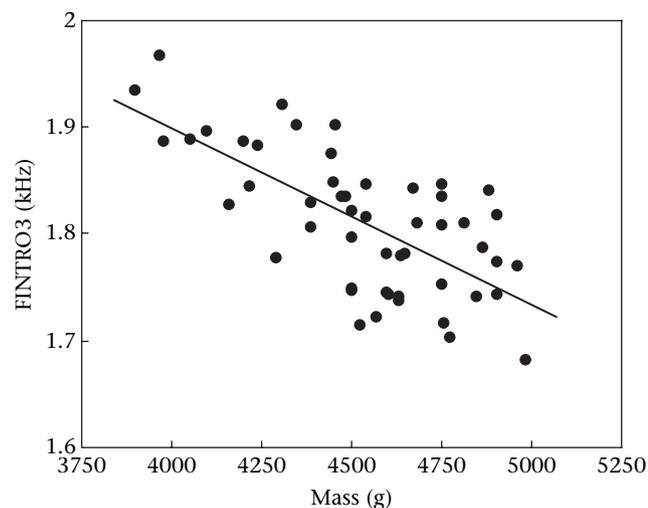

Figure 2. Regression plotting the dominant frequency of the third note of the introductory phrase of the yodel (FINTRO3) as a function of male body mass (slope with removal of one outlier = 0.0002; $r^2 = 0.437$; $N = 54$ males; $P < 0.0001$).
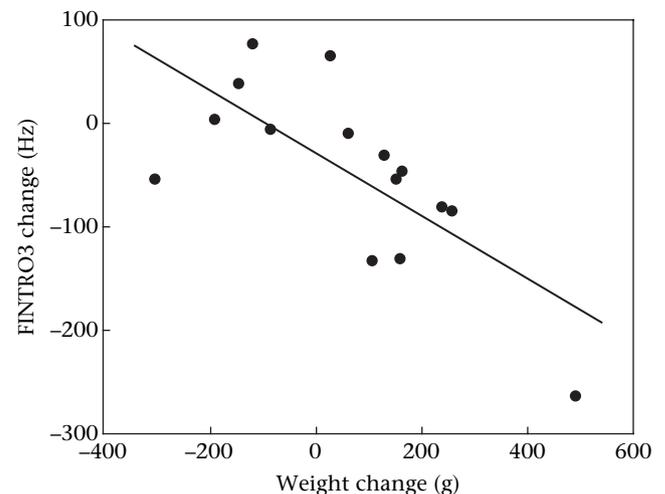

Figure 3. Relationship between the change in the dominant frequency of the third note of the introductory phrase of the yodel (FINTRO3) with changes in loon body mass for 15 males caught multiple times between 2001 and 2005 (slope = −0.305, $r^2 = 0.518$, $N = 15$ males, $P = 0.0025$).

Table 3. Mean values ± 1 SE for acoustic responses of 42 pairs of common loons following broadcast yodels from unfamiliar loons that were unmanipulated, or manipulated to be either about 200 Hz higher (high-pitch) or about 200 Hz lower (low-pitch) in frequency

	Treatment			Friedman ANOVA
Response	Low-pitch	Unmanipulated	High-pitch	P
Univariate response ($\overline{X}$ number)				
Vocalizations	17.83±4.90	15.52±4.51	8.12±2.53	0.0279, H/L**
Tremolos	12.26±4.66	12.05±4.13	5.55±2.16	0.4305
Wails	4.02±0.67	2.36±0.76	1.50±0.59	0.0017, H/L**, L/U*
Yodels	1.57±0.34	1.05±0.35	1.05±0.39	0.0061, H/L*, L/U*
Latency before first vocalization (s)	89.79±29.38	156.00±44.80	146.67±44.18	<0.0001, H/L***, L/U***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$, from post hoc Wilcoxon Z tests between unmanipulated (U), manipulated-high-frequency (H), or manipulated-low-frequency (L) groups.

heed signals that reflect fighting ability and aggressive motivation of territorial males. We might expect, then, that territorial flyovers and intrusions, which occur several times a day during the breeding season, would allow prebreeders to assess (1) territory quality, based on the presence or absence of chicks (Piper et al. 2006) and (2) fighting ability and motivation of territorial males, based upon the vocal responses of territory owners. Collecting such information without direct contact with territory owners may reduce the risk of costly and dangerous visits to territories.

Our results suggest that the dominant frequency of the yodel is an honest signal of male body mass and condition. Body mass appears to be directly related to fighting ability, because heavier males hold their breeding territories for long periods (Piper et al. 2000) and tend to occupy territories of historically higher reproductive success (Evers 2001). Hence, a prebreeding male searching for a small, vulnerable territory holder might learn which territories he could take over by listening to the yodels of territorial owners. In this context, the yodel serves as a signal that permits assessment of male quality.

What Costs/Constraints Maintain Signal Honesty?

Like many signals, the yodel may have evolved to effectively communicate information that mutually benefits both signallers and intended receivers. As a territorial signal, certain elements of the yodel may be selectively maintained to provide reliable information about a male's identity and location (Endler 1993; Bradbury & Vehrencamp 1998). However, as a threat signal, the yodel also may reflect a male's fighting ability and motivational state (Bradbury & Vehrencamp 1998; ten Cate et al. 2002). The territorial yodel appears to be quite dynamic, in that it contains elements that communicate identity (Walcott et al. 1999), aggressive motivation (Barklow 1979a; McIntyre 1988), and male fighting ability (this study). As such, in a single vocalization the yodel provides information necessary for other conspecifics (both males and females) to assess the identity, competitive ability and aggressive motivation of the signaller.

If dominant frequencies reliably communicate male fighting ability, it is intriguing to consider what selective pressures are responsible for maintaining signal honesty among yodelling individuals. Preliminary observations indicate that smaller territorial residents (with higher-frequency yodels) are more reluctant to yodel than larger individuals are when conspecifics fly over and/or intrude upon their territories (logistic regression: $r^2 = 0.23$, $N = 27$ males, $P < 0.01$; J. Mager, unpublished data). When they do yodel, individuals having higher-frequency yodels tend to give longer yodels ($r^2 = 0.15$, $N = 53$ males, $P < 0.01$; J. Mager, unpublished data) that in turn are likely to reflect more aggressive motivational states (Barklow 1979a). Although smaller males tend to produce higher-frequency yodels, and individuals that produce higher-frequency yodels tend to produce longer yodels, yodel duration is not correlated either with male body mass ($r_{53} = -0.206$, males, $P = 0.13$), or with condition ($r_{53} = -0.263$, $P = 0.06$; J. Mager, unpublished data). This raises the possibility that high-frequency yodellers (which tend to be smaller) may recognize that signalling at such frequencies might be disadvantageous, and consequently yodel when they must (i.e. when their motivation is high), but at the same time reveal information about their potentially weaker condition-dependent fighting abilities.

This hypothesis, in turn, raises the question that, if smaller individuals could 'cheat' by producing deceptive low-frequency yodels, would they be more likely to yodel at intruders flying over their territories regardless of motivational state? Perhaps the dominant frequencies that loons produce are constrained by physical size or physiological condition, such that smaller individuals are physically or physiologically unable to produce lower-frequency yodels (index signal; Vehrencamp 2000). Alternatively, low frequencies may be costlier to produce, and larger individuals are able to handle these costs (handicap signal; Vehrencamp 2000), or there may be no cost or constraints of signal production, but honesty is maintained by arbitrary 'rules' where receiver retaliation prevents bluffing (conventional signal; Vehrencamp 2000). Considering these possibilities will require more empirical investigations of both receiver-independent and receiver-dependent costs (Bradbury & Vehrencamp 1998; Vehrencamp 2000) of producing low-frequency yodels.

Acoustic signals in which elements are correlated with measures of body size are prevalent among mammals (e.g. Clutton-Brock & Albon 1979; August & Anderson 1987; Gouzoules & Gouzoules 1990), amphibians (e.g. Davies & Halliday 1978; Robertson 1986) and birds (e.g. Barabraud et al. 2000). The correlation between body size and the dominant frequencies that birds produce has been attributed to the allometric relationship between body size and the size of the avian syrinx (Morton 1975, 1977; Ryan & Brenowitz 1985). Consequently, the fundamental frequencies that many birds produce are constrained to some extent by body size (Morton 1977; Ryan & Brenowitz 1985). At a macrogeographical scale, variability in the dominant frequencies that male loons produce can be explained by body size, as the dominant frequencies are correlated with structural body size and mass (McIntyre, 1988; J. Mager, unpublished data); however, at a microgeographical scale variability in male body condition, not structural body size, accounts for variation in dominant frequencies. Such relationships between the dominant frequencies of assessment signals and male body condition, rather than structural body size, exist among other nonpasserine birds, both in the context of male–male competition and female attraction. For example, correlations between unmodulated elements of the territorial advertisement 'perch coo' vocalization and body mass (which reflects male quality) have been observed among collared doves, *Streptopilia decaocto*, although the degree of modulation of these frequencies, and not the dominant frequencies themselves, appears to be important for advertisement of male quality (Slabbekoorn & ten Cate 1996, 1997, 1998). However, among little penguins, *Eudyptula minor*, Miyazaki & Waas (2003) not only found a significant relationship between male mass (and not structural body size) and properties of the exhalation properties of advertisement calls, but also that females were more responsive to low- and medium-pitched calls. Similarly, regardless of their potential importance in male–male competition and/or female attraction, constraints associated with physical condition, not structural body size, appear to better explain variation in the dominant frequencies of the loon's yodel.

Physiological costs and/or constraints associated with male condition may indeed influence the dominant frequencies that loons can produce. The dominant frequencies that birds incorporate into acoustic signals can be influenced by syringeal membrane mass, thickness and tension, by tracheal size and shape (Gaunt & Gaunt 1985; Fletcher & Tarnopolsky 1999; Palacios & Tubaro 2000), and by syringeal muscle condition (Goller & Suthers 1996a, b) and hormones (Beani et al. 1995). Without an understanding of the mechanisms responsible for sound production in loons, especially those responsible for variability in the dominant frequencies, our ideas regarding the physical costs or physiological constraints of sound production in loons are speculative. However, we hope that future investigations will consider such possibilities to develop a better understanding of these communication systems and their contributions to the dynamics of loon territorial behaviour.

References

Appleby, B. M. & Redpath, S. M. 1997. Indicators of male quality in the hoots of tawny owls (*Strix aluco*). *Journal of Raptor Research*, **31**, 65–70.

August, P. V. & Anderson, J. G. T. 1987. Mammal sounds and motivation-structural rules: a test of the hypothesis. *Journal of Mammalogy*, **68**, 1–9.

Barabraud, C., Mariani, A. & Jouventin, J. 2000. Variation in call properties of the snow petrel, *Pagodroma nivea*, in relation to sex and body size. *Australian Journal of Zoology*, **48**, 421–430.

Barklow, W. E. 1979a. The function of variations in the vocalizations of the common loon (*Gavia immer*). Ph.D. thesis, Tufts University.

Barklow, W. E. 1979b. Graded frequency variations of the tremolo call of the common loon (*Gavia immer*). *Condor*, **81**, 53–64.

Barklow, W. E. 1988. The structure and function of the wail call of the common loon. In: *Papers from the 1987 Conference on Loon Research and Management* (Ed. by P. I. V. Strong), pp. 53. Meredith, New Hampshire: North American Loon Fund.

Beani, L. & Dessì-Fulgheri, F. 1995. Mate choice in the grey partridge, *Perdix perdix*: role of physical and behavioural male traits. *Animal Behaviour*, **49**, 347–356.

Beani, L., Panzica, G., Briganti, F., Persichella, P. & Dessì-Fulgheri, F. 1995. Testosterone-induced changes in call structure, midbrain and syrinx anatomy in partridges. *Physiological Behavior*, **58**, 1149–1157.

Bertelli, S. & Tubaro, P. L. 2002. Body mass and habitat correlates of song structure in a primitive group of birds. *Biological Journal of the Linnean Society*, **77**, 423–430.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.

Bretagnolle, V. 1989. Calls of Wilson's storm-petrel: functions, individual and sexual recognitions and geographic variation. *Behaviour*, **11**, 98–112.

Brown, M. E. 1996. Assessing body condition in birds. In: *Current Ornithology. Vol. 18* (Ed. by V. Nolan, Jr & E. D. Ketterson), pp. 67–135. New York: Plenum.

Clutton-Brock, T. H. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaivour*, **69**, 145–170.

Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.

Endler, J. A. 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 215–225.

Evers, D. C. 1993. A replicable capture method for adult and juvenile common loons on their nesting lakes. In: *Proceedings from the 1992 Conference on the Loon and Its Ecosystem: Status, Management, and Environmental Concerns* (Ed. by F. Stockwell), pp. 214–220. Holderness, New Hampshire: North American Loon Fund.

Evers, D. C. 2001. Common loon population studies: continental mercury patterns and breeding territory philopatry. Ph.D. thesis, University of Minnesota.

Fletcher, N. H. & Tarnopolsky, A. 1999. Acoustics of the avian vocal tract. *Journal of the Acoustical Society of America*, **105**, 35–49.

Furlow, B., Kimball, R. T. & Marshall, M. C. 1998. Are rooster crows honest signals of fighting ability? *Auk*, **115**, 763–766.

Gaunt, A. S. & Gaunt, S. L. L. 1985. Syringeal structure and avian phonation. In: *Current Ornithology. Vol. 2* (Ed. by R. F. Johnson), pp. 213–245. New York: Plenum.

Genevois, F. & Bretagnolle, V. 1994. Male blue petrels reveal their body mass when calling. *Ethology, Ecology and Evolution*, **6**, 377–383.

Goller, F. & Suthers, R. A. 1996a. Role of syringeal muscles in gating airflow and sound production in singing brown thrashers. *Journal of Neurophysiology*, **75**, 867–876.

Goller, F. & Suthers, R. A. 1996b. Role of syringeal muscles in controlling the phonology of bird song. *Journal of Neurophysiology*, **76**, 287–300.

Gouzoules, H. & Gouzoules, S. 1990. Body size effects on the acoustic structure of pigtail macaque (*Macaca nemestrina*) screams. *Ethology*, **85**, 324–334.

Johnson, M. 2002. Individual growth analysis using PROC MIXED. *Proceedings of the Twenty-seventh Annual SAS Users Group International Conference.* Paper 253–27. Cary, North Carolina: SAS Institute.

Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour*, **61**, 1029–1033.

Lindsay, A. R. 2002. Molecular and vocal evolution in loons (Aves: Gaviiformes). Ph.D. thesis, University of Michigan.

McIntyre, J. W. 1988. *The Common Loon: Spirit of Northern Lakes.* Minneapolis: University of Minnesota Press.

McIntyre, J. W. 1994. Loons in freshwater lakes. *Hydrobiologia*, **279/280**, 393–413.

McIntyre, J. W. & Barr, J. F. 1997. Common loon (*Gavia immer*). In: *Birds of North America. No. 313* (Ed. by A. Poole & F. Gill), Philadelphia: Academy of Natural Sciences; Washington, D.C.: American Ornithologists' Union.

Mager, J. N. 2000. The effect of chick age and brood size upon parental effort within breeding common loons (*Gavia immer*). In: *Loons: Old History and New Findings* (Ed. by J. W. McIntyre & D. C. Evers), pp. 55–65. Holderness, New Hampshire: North American Loon Fund.

Miyazaki, M. & Waas, J. R. 2003. Acoustic properties of male advertisement and their impact on female responsiveness in little penguins *Eudyptula minor*. *Journal of Avian Biology*, **34**, 229–232.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**, 403–405.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.

Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.

Olson, S. T. & Marshall, W. H. 1952. *The Common Loon in Minnesota.* Minneapolis: University of Minnesota Press.

Palacios, M. G. & Tubaro, P. L. 2000. Does beak size affect acoustic frequencies in woodpeckers? *Condor*, **93**, 644–658.

Paruk, J. D. 1999. Territorial take-over in *Gavia immer*. *Wilson Bulletin*, **111**, 116–117.

Piersma, T. & Davidson, N. C. 1991. Confusions of mass and size. *Auk*, **108**, 441–444.

Piper, W. H., Evers, D. C., Meyer, M. W., Tischler, K. B., Kaplan, J. D. & Fleischer, R. C. 1997. Genetic monogamy in the common loon (*Gavia immer*). *Behavioral Ecology and Sociobiology*, **41**, 25–31.

Piper, W. H., Tischler, K. B. & Klich, M. 2000. Territory acquisition in loons: the importance of take-over. *Animal Behaviour*, **59**, 385–394.

Piper, W. H., Walcott, C., Mager, J. N., III, Perala, M., Tischler, K. B., Harrington, E. B., Turcotte, A. J., Schwabenlander, M. & Banfield, N. 2006. Prospecting in a solitary breeder: chick production elicits territorial intrusions in common loons. *Behavioral Ecology*, **17**, 881–888.

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, **409**, 185–188.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Robertson, J. G. M. 1986. Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. *Animal Behaviour*, **34**, 763–772.

Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, **126**, 87–100.

Schulte-Hostedde, A. L., Zinner, B., Millar, J. S. & Hickling, G. J. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology*, **86**, 155–163.

Singer, J. D. 1998. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Education and Behavioral Statistics*, **24**, 323–355.

Sjölander, S. & Årgen, G. 1972. Reproductive behavior of the common loon. *Wilson Bulletin*, **81**, 296–308.

Slabbekoorn, H. & ten Cate, C. 1996. Responses of collared doves to playback of coos. *Behavioural Processes*, **38**, 169–174.

Slabbekoorn, H. & ten Cate, C. 1997. Stronger territorial responses to frequency modulated coos in collared doves. *Animal Behaviour*, **54**, 955–965.

Slabbekoorn, H. & ten Cate, C. 1998. Perceptual tuning to frequency characteristics of territorial signals in collared doves. *Animal Behaviour*, **56**, 847–857.

ten Cate, C., Slabbekoorn, H. & Ballintijn, M. R. 2002. Birdsong and male–male competition: causes and consequences of vocal variability in the collard dove *Streptopelia decaocto*. *Advances in the Study of Behavior*, **31**, 31–75.

Tubaro, P. L. & Mahler, B. 1998. Acoustic frequencies and body mass in New World doves. *Condor*, **100**, 54–61.

Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal Signals: Signaling and Signal Design in Animal Communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277–300. Trondheim, Norway: Tapir Academic Press.

Vogel, H. S. 1995. Individuality in, and discrimination through, the two-note wail and yodel calls of the common loon (*Gavia immer*). M.S. thesis, University of Guelph.

Wagner, W. E., Jr. 1989. Fighting, assessment and frequency of alteration in Blanchard's cricket frog. *Behavioral Ecology and Sociobiology*, **25**, 429–436.

Walcott, C., Evers, D. C., Froehler, M. & Krakauer, A. 1999. Individuality in 'yodel' calls recorded from a banded population of common loons, *Gavia immer*. *Bioacoustics*, **10**, 101–114.

Wallschläger, D. 1980. Correlation of song frequency and body weight in passerine birds. *Experientia*, **36**, 412.

Wentz, L. E. 1990. Aspects of the nocturnal vocal behavior of the common loon (Aves: *Gavia immer*). Ph.D. thesis, Ohio State University.

Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 147–208. New York: Academic Press.