Macrogeographic Variation in the Body Size and Territorial Vocalizations of Male Common Loons (*Gavia immer*)

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Abstract.—Geographic variation in the body mass and acoustic parameters of territorial 'yodels' recorded from male Common Loons (*Gavia immer*) were assessed for individuals breeding on territories across the eastern United States. Multivariate analyses incorporating male body mass, body size, the acoustic parameters of yodels, and geographic latitude and longitude indicated that males inhabiting lakes in northwestern regions were smaller and produced higher-frequency yodels. These relationships strengthen previous observations of clinal geographic variation in loon body size and vocal behavior across North America, but also support the hypothesis that the dominant frequencies of yodels are in part influenced by male body size. Therefore, the frequencies loons use for long-distance communication are apparently influenced, at least in part, by those selective forces responsible for shaping optimal body size. *Received 8 February 2006, accepted 29 October 2006.*

Key words.—Common Loon, *Gavia immer*, vocalization, yodel, geographic variability.

Many birds use acoustic signals to communicate their species and individual identity, fighting ability, physical condition, and/or motivational intent (Bradbury and Vehrencamp 1998). The acoustic structure of such signals can vary across either a limited or broad geographic range. Macrogeographic variation, or variation in signal structure between populations that experience reduced gene flow or transmission of cultural traditions, has long been of interest among scientists, particularly to those interested in biological evolution of song dialects (Mundinger 1982; Catchpole and Slater 1995). Much research of macrogeographic variability in bird vocalizations has been restricted to oscines, and has focused mainly on regional differences in syllable repertoires (Mundinger 1982). Relatively few have considered such macrogeographic variation among nonoscine species (e.g., Bretagnolle 1996; Bradbury *et al.* 2001), or the biological forces responsible for such variation.

Common Loons (*Gavia immer*) have a vocal repertoire atypical of most, if not all, noncolonial monogamous waterbirds (McIntyre and Barr 1997). The yodel (Fig. 1) is the most structurally complex of the loon vocal repertoire, and is given exclusively by males primarily on territories during the breeding season (Barklow 1979; McIntyre 1988; McIntyre and Barr 1997). The yodel is believed to be a long-range threat signal, as it is given primarily during aggressive situations and territorial encounters (Olson and Marshall 1952; Sjølander and Årgen 1972; Rummel and Goetzinger 1975, 1978). Males yodel most frequently within a two-week period after they return to breeding territories (McIntyre 1988); however, there is also a notable peak in diurnal yodeling rate prior to hatching (Mager, unpublished data). Structural analyses (e.g., Barklow 1979; Vogel 1995; Walcott *et al.* 1999; Walcott and Evers 2000; Lindsay 2002) have revealed considerable variability among the yodels of territorial males. The finding that some elements within the yodel exhibit low intra-individual variability and high inter-individual variability, as well as the finding that territorial loons respond differently to yodels from territorial neighbors and non-neighbors (Vogel 1995; Lindsay 2002) suggest one of its functions is to communicate information about individual identity. Barklow (1979), however, suggested that in addition to individual recognition, features of the yodel (specifically the number of repeat phrases) likely communicate informa-
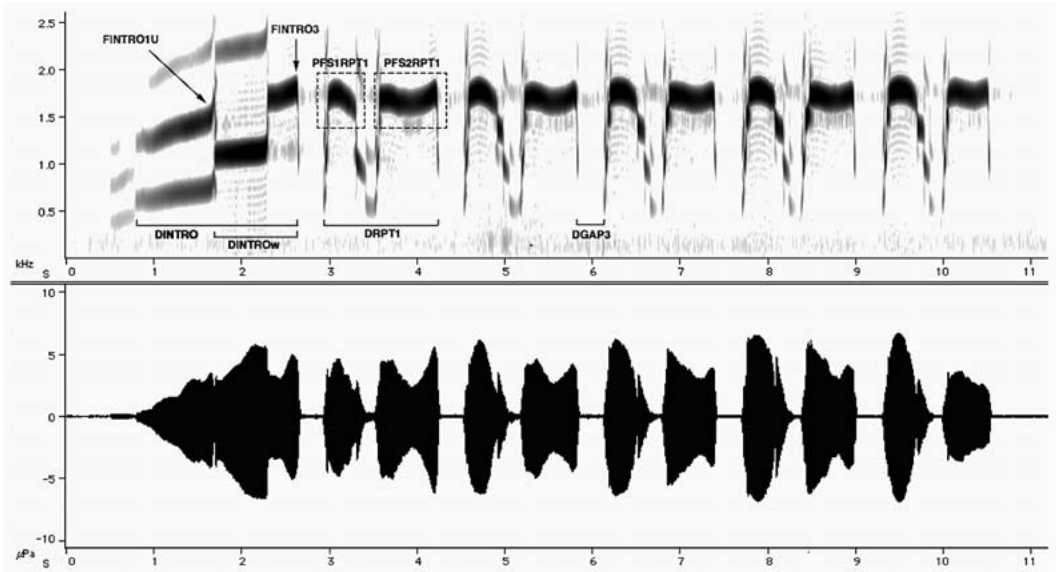
Figure 1. Acoustic spectrogram (above), showing the change in frequency (in kHz) and oscillogram (below), showing the change in energy (in µPa) of a typical yodel over time (in sec). Structurally, the yodel consists of two fundamental features: an introductory phrase of three-four notes that rise in frequency, and a motif of two-syllable repeat phrases following the introductory phrase.

tion about a male's aggressive 'motivation' or willingness to escalate a contest. Additionally, the yodel may convey information about male quality or condition, as elements that exhibit high inter-individual variability may have been shaped by condition-dependent selective forces (Lindsay 2002). Therefore, the yodel may be quite dynamic in that it can communicate the identity, quality, and motivation of a territorial male.

There is considerable geographic variability among individual parameters of the yodel across North America. Focusing on two syllables of the first repeat phrase, McIntyre (1988) found males from Saskatchewan, Minnesota, and New York produced yodels of different peak frequencies (i.e., those of highest relative amplitude). Following Morton (1977), McIntyre (1988) attributed these differences to differences in male body size, as Common Loons that breed further inland tend be smaller (Rand 1947). However, this idea has not been examined thoroughly in terms of the many yodel parameters that are ideal candidates for long-distance communication, the number of individuals surveyed, nor the number of locations from which individuals were surveyed along a geographic range.

The present study addressed these issues by providing a more extensive survey of geographical variability in the yodel by assessing variability in many acoustic features across the eastern United States. Specifically, the aims of this study were to: 1, more thoroughly assess geographic variability in yodel structure by not only measuring those variables considered by McIntyre (1988), but also additional duration, latency (i.e., the duration of the time between elements), and frequency features, 2, to consider more individuals located at various areas within the eastern United States, and 3, indirectly analyze relationships between these features and body size and weight from data published from previous studies as well as from recently obtained measures of body mass.

STUDY SITE AND METHODS

Research was conducted on freshwater lakes of the eastern United States where Common Loons breed (Maine, New Hampshire, Vermont, New York, Michigan, Wisconsin, and Minnesota, geographic range: 43.716°-48.181°N latitude and 070.632°-092.146°W longitude)

during the summer of 2000. Males were identified from their unique combinations of colored leg bands (see Evers 1993). Yodels were recorded using two methods: 1, *in situ* recording during behavioral observations in the field, and 2, recording responses to recorded playbacks of other Common Loon vocalizations. Yodels were recorded onto digital audio tape (DAT) using a Sennheiser MKH-70 shotgun microphone and HHB PortaDAT recorder at a sampling rate of 44.1 kHz. Recorded yodels were downloaded and converted into digital audio (AIFF) files using the Canary sound analysis software package (v. 1.5, Cornell University Bioacoustics Research Program). Recordings were Fourier transformed (using a 349.7 Hz bandwidth, 4,096 points per frame, 50% frame overlap in successive transforms, and a Hamming sampling window) to generate spectrograms from which frequency (nearest Hz), latency (time, to the nearest 0.001 between elements), and duration (nearest 0.001 s) parameters (Table 1) were measured.

To explore the general association among the 19 yodel parameters and geographic location (latitude and longitude, determined to the nearest 0.001 degree from GPS and USGS map coordinates), covariance between these variables was measured by calculating product-moment correlation coefficients. Multiple regression analyses were used to: 1, investigate whether variability in yodel parameters could be described as a function of the independent variables of latitude and longitude together, and 2, calculate partial regression coefficients to determine whether either geographic variable could explain such variability independently.

Relationships between yodel parameters and loon body size were considered by analyzing variability in yodel parameters of recently recorded calls with previously published data (Storer 1988) of geographic variability in body size across the region. These assessments were conducted by first classifying yodels into three geographic regions Storer (1988) had previously considered: 55-75°, 76-85°, and 86-95°W longitude south of 55°N latitude. MANOVA was then implemented to assess significant differences among yodel parameters between regions. Relationships between loon body mass and yodel parameters were assessed from multiple regression analysis body masses gathered from adults we captured and weighed to the nearest g. Unless noted otherwise, statistical significance was accepted at $\alpha <$ 0.05. However, to reduce the likelihood of falsely rejecting one of the many null hypotheses associated with each independent parameter being tested while maintaining adequate statistical power by multiple correlation analysis, sequential Bonferroni corrections (Rice 1989) were used to reduce α for rejection of the null hypothesis that any two variables were not correlated (however, see Moran 2003; Nakagawa 2004).

RESULTS

Of the 337 yodels recorded from 49 individuals (mean yodels recorded per individual = 7, range: 2-20), there was great variation among frequency and duration parameters, and significant correlations among a number of these parameters (Bartlett's test for sphericity $\chi^2 = 1,436.894$, $P < 0.0001$). All frequency parameters were highly correlated with each other; however, there was little correlation among duration parameters (Table 2). As expected, the yodel duration was strongly correlated with the number of re-

Table 1. Definitions of measured and calculated parameters of yodels recorded from Common Loons.

Parameter	Definition
Measured parameters	
DENT	Duration (in sec) of entire yodel
DINTRO	Duration (in sec) of introductory phrase
DINTRO$_w$	Duration (in sec) of second and third notes of introductory phrase
DGAP$_x$	Latency (in sec) of time before repeat phrase x
DRPT$_x$	Duration (in sec) of entire repeat phrase x
FINTRO1U	Frequency (in kHz) with highest intensity at end of second harmonic of first note of introductory phrase
FINTRO3	Frequency (in kHz) with highest intensity at end of third note of introductory phrase
PFINTRO3	Peak frequency (in kHz) of entire third note of introductory phrase
PFALLRPT	Peak frequency (in kHz) of entire motif of repeat phrases
PFRPT$_x$	Peak frequency (in kHz) of repeat phrase x
PFS$_1$RPT$_x$	Peak frequency (in kHz) of first syllable of repeat phrase x
PFS$_2$RPT$_x$	Peak frequency (in kHz) of second syllable of repeat phrase x
Calculated parameters	
#R	Number of repeat phrases in entire yodel
MDRPT	Mean duration (in sec) of a repeat phrase
MPFRPT	Mean peak frequency (in kHz) of a repeat phrase
MPFSYL	Mean peak frequency (in kHz) of a repeat syllable
MDGAP	Mean latency of time (in sec) before each repeat syllable
MΔDGAP	Mean change in latency (in sec) of between successive GAPs
MΔDRPT	Mean change in duration (in sec) of successive repeat phrases

Table 2. Correlation coefficients (r) from analysis of 19 parameters measured from the yodels of 49 male Common Loons. See Table 1 for parameter definitions. * = significant relationship at a sequential Bonferroni-corrected α of 0.05.

	DENT	#R	DINTRO	DIN-TRO$_w$	DGAP$_1$	FIN-TRO1U$_w$	FIN-TRO3$_w$	PFIN-TRO3	PFALL-RPT	DRPT$_1$	PFRPT$_1$	PFS$_1$RPT$_1$	PFS$_2$RPT$_1$	MDRPT	MDGAP	MPFRPT	MPFSYL	MΔD-GAP
#R	0.921*																	
DINTRO	0.109	-0.162																
DIN-TRO$_w$	-0.094	-0.309	0.661*															
DGAP$_1$	-0.183	-0.273	-0.037	-0.083														
FIN-TRO1U$_w$	-0.024	0.075	-0.123	-0.429	-0.116													
FIN-TRO3$_w$	0.108	0.238	-0.062	-0.215	-0.177	0.734*												
PFIN-TRO3	0.099	0.228	-0.098	-0.316	-0.179	0.751*	0.860*											
PFALL-RPT	0.008	0.097	-0.033	-0.156	-0.136	0.683*	0.827*	0.783*										
DRPT$_1$	-0.021	-0.337	0.512*	0.547*	0.156	-0.256	-0.332	-0.397	-0.272									
PFRPT$_1$	0.003	0.143	-0.082	-0.207	-0.184	0.772*	0.935*	0.859*	0.896*	-0.359								
PFS$_1$RPT$_1$	-0.022	0.109	-0.027	-0.190	-0.181	0.724*	0.922*	0.864*	0.844*	-0.277	0.920*							
PFS$_2$RPT$_1$	0.051	0.178	-0.075	-0.147	-0.167	0.667*	0.904*	0.801*	0.863*	-0.344	0.910*	0.845*						
MDRPT	0.001	-0.323	0.519*	0.535*	0.176	-0.286	-0.340	-0.415	-0.278	0.959*	-0.360	-0.319	-0.351					
MDGAP	0.036	-0.114	-0.034	-0.132	0.541*	-0.157	-0.167	-0.114	-0.088	0.190	-0.175	-0.160	-0.118	0.232				
MPFRPT	0.031	0.149	-0.043	-0.154	-0.233	0.734*	0.897*	0.791*	0.912*	-0.293	0.927*	0.890*	0.922*	-0.332	-0.241			
MPFSYL	0.038	0.156	-0.075	-0.146	-0.220	0.736*	0.922*	0.793*	0.913*	-0.277	0.934*	0.907*	0.938*	-0.300	-0.168	0.970*		
MΔD-GAP	-0.124	-0.049	0.036	0.103	-0.219	0.116	0.041	0.014	0.053	0.190	0.078	0.097	0.067	-0.209	-0.546*	0.091	0.085	
MΔD-RPT	0.124	0.041	0.178	0.226	-0.070	-0.089	-0.072	-0.098	-0.047	-0.170	-0.118	0.043	0.010	0.226	-0.041	0.085	-0.168	0.056

peat phrases (Table 2). However, duration measures of the introductory phrase (DINTRO and $DINTRO_W$) were significantly correlated with the duration of the first repeat phrase ($DRPT_1$) and the mean duration of all repeat phrases (Table 2).

Qualitatively, the basic structure of the yodel with respect to both the introductory phrase and the motif of 2-syllable repeat phrases did not vary across latitude or longitude, i.e., there was no introduction nor removal of novel elements to the basic yodel structure. Geographically, variation in many frequency elements, but not in any duration or latency elements, corresponded to location (Table 3). In many instances, longitude, not latitude, was the better predictor of variation in these components, as the standardized regressions were significant and the partial regression coefficients for longitude were higher than those for latitude (Table 3). Multiple regression analyses of body mass across this region indicate loon body mass varies similarly across the same geographic rage: loons that breed on more western lakes tend to be lighter (Table 3). Consequently,

geographic variation in the dominant frequencies loons produced corresponded with geographic decreases in male wing and tarsus lengths (Table 4).

DISCUSSION

The results of this study strengthen McIntyre's (1988) findings that loons breeding on more easterly lakes produced lower-frequency repeat phrases in their yodels. However, in addition to lower-frequency repeat phrases, the present study identified similar clinal geographic patterns for all frequency elements that may be important for long-distance communication. Longitude was far better than latitude at explaining variation in dominant frequencies. Although significant correlations among few duration parameters of individual yodels existed, there were no relationships between the duration parameters and geographical location. The strong relationship between yodel duration and number of repeat phrases provides empirical support that yodel duration is the product of the number of repeat phrases giv-

Table 3. Results of multiple regression analysis considering variation in loon body mass and yodel parameters (N = 49 males) with latitude and longitude, as well as partial regression coefficients (r) of each parameter with latitude and longitude. See Table 1 for parameter definitions.

Parameter	Latitude and Longitude			Latitude			Longitude		
	r^2	$F_{2,46}$	P	r	t	P	r	t	P
Body Mass	0.76	400.51	<0.0001	-0.04	-0.88	0.38	-0.84	16.59	<0.0001
DENT	0.04	1.09	0.35	-0.33	-1.39	0.17	0.19	0.80	0.43
#R	0.16	0.58	0.56	-0.26	-1.08	0.29	0.21	0.87	0.39
DINTRO	0.04	0.88	0.42	0.28	1.17	0.25	-0.31	-1.31	0.20
$DINTRO_w$	0.15	4.05	0.02	0.32	0.16	0.88	-0.58	-2.63	0.01
$DGAP_1$	0.04	1.05	0.36	-0.33	-1.42	0.16	0.31	1.31	0.20
FINTRO1U	0.61	35.79	<0.0001	0.17	1.13	0.26	0.64	4.24	0.0001
$FINTRO3_w$	0.56	29.27	<0.0001	0.31	1.97	0.06	0.48	2.96	0.0047
PFINTRO3	0.59	32.39	<0.0001	0.35	2.23	0.03	0.46	2.97	0.0047
PFALLRPT	0.59	32.43	<0.0001	0.35	2.23	0.03	0.46	2.98	0.0045
$DRPT_1$	0.10	2.47	0.10	-0.23	-0.99	0.33	-0.10	-0.44	0.67
$PFRPT_1$	0.67	47.55	<0.0001	0.47	3.44	0.001	0.39	2.87	0.0062
PFS_1RPT_1	0.61	35.36	<0.0001	0.39	2.57	0.01	0.44	2.89	0.0058
PFS_2RPT_1	0.55	28.22	<0.0001	0.42	2.61	0.01	0.36	2.26	0.0289
MDRPT	0.10	2.61	0.08	-0.16	-0.71	0.48	-0.18	-0.77	0.45
MDGAP	<0.01	0.01	0.99	0.03	0.12	0.91	-0.02	-0.08	0.94
MPFRPT	0.60	22.71	<0.0001	0.28	1.80	0.08	0.53	3.49	0.0011
MPFSYL	0.60	34.28	<0.0001	0.34	2.22	0.03	0.48	3.13	0.0030
MΔDGAP	<0.01	0.04	0.96	-0.07	-0.28	0.78	0.06	0.23	0.82
MΔDRPT	0.08	2.00	0.15	-0.42	-1.81	0.08	0.21	0.92	0.36

Table 4. Variation in the yodel parameters (N = 49 males) and body size[a] of male Common Loons breeding in three different longitudinal regions. Values represent means ± 1 SE.

Measurement	55-75°W	76-85°W	86-95°W	$F_{2,46}$	P
Body Measurement[a]					
Wing Length	368.7	363.1	361.2		
Tarsus Length	91.4	90.5	89.7		
Bill to Nostril	18.0	19.1	18.1		
Bill from Nostril	64.5	63.3	63.7		
Bill Depth	24.6	24.7	24.0		
Yodel Parameter[b]					
DENT	7.372 ± 0.386	6.790 ± 0.360	7.044 ± 0.334	0.343	0.7114
DINTRO	1.891 ± 0.062	1.943 ± 0.064	1.827 ± 0.047	0.743	0.4814
$DINTRO_w$	1.184 ± 0.056	1.096 ± 0.076	1.035 ± 0.030	3.341	0.0442
$DGAP_1$	0.242 ± 0.007	0.254 ± 0.017	0.245 ± 0.006	0.338	0.7151
$DRPT_1$	1.184 ± 0.046	1.137 ± 0.042	1.096 ± 0.022	1.969	0.1512
FINTRO1U	1.350 ± 0.014	1.471 ± 0.025	1.502 ± 0.012	32.712	<0.0001
FINTRO3	1.706 ± 0.015	1.855 ± 0.019	1.952 ± 0.030	20.057	<0.0001
PFINTRO3	1.619 ± 0.025	1.803 ± 0.033	1.886 ± 0.029	21.399	<0.0001
PFALLRPT	1.593 ± 0.039	1.748 ± 0.014	1.867 ± 0.024	22.208	<0.0001
$PFRPT_1$	1.610 ± 0.019	1.751 ± 0.021	1.866 ± 0.025	28.543	<0.0001
PFS_1RPT_1	1.684 ± 0.016	1.783 ± 0.022	1.908 ± 0.024	24.453	<0.0001
PFS_2RPT_1	1.597 ± 0.024	1.746 ± 0.015	1.839 ± 0.030	17.573	<0.0001
#R	3.847 ± 0.335	3.419 ± 0.250	3.814 ± 0.263	0.263	0.7701
MDRPT	1.182 ± 0.040	1.133 ± 0.043	1.102 ± 0.018	2.116	0.1262
MPFRPT	1.610 ± 0.026	1.747 ± 0.018	1.864 ± 0.026	23.678	<0.0001
MPFSYL	1.621 ± 0.019	1.753 ± 0.014	1.850 ± 0.025	22.652	<0.0001
MDGAP	0.269 ± 0.008	0.281 ± 0.023	0.270 ± 0.009	0.151	0.8607
MΔDGAP	-0.014 ± 0.004	-0.109 ± 0.098	-0.008 ± 0.009	3.396	0.0421
MΔDRPT	0.014 ± 0.008	0.002 ± 0.003	<0.001 ± 0.009	0.673	0.5149

[a]Measurements (in mm) reported by Storer (1988). Statistical differences were not reported.
[b]Refer to Table 1 for definition and units of each abbreviated parameter.

en. Longer yodels likely enhance signaler detectability (Wiley and Richards 1982), which in turn supports the hypothesis that the number of repeats phrases may functionally reflect a male's greater willingness to escalate a contest (see Barklow 1979).

Avian acoustic signals have been evolutionarily shaped to optimize sound generation and emission, propagation, and reception, and variation in signal structure often reflects adjustments by individuals to efficiently transmit information between signalers and receivers (Endler 1993; Bradbury and Vehrencamp 1998). Many studies of intraspecific macrogeographic variation in the dominant frequencies of bird song have concentrated on adjustments made in response to the unique transmission properties of terrestrial (Morton 1975; Wiley and Richards 1982) and aquatic (McIntyre 1994) environments. While similarity in the basic acoustic structure of the yodel across the geographic range can be explained by species-specific selective factors (Mundinger 1982), the range of dominant frequencies that loons incorporate into yodels may be partially influenced by transmission properties of the environment. Specifically, because dominant frequencies fall within a range that experiences minimum excessive attenuation (Morton 1975; Wiley and Richards 1982; McIntyre 1994), it cannot be discounted that the yodel in part has evolved to effectively transmit information across an extensive geographic range.

However, as proposed by McIntyre (1998) and supported with a more rigorous study here, variability in the dominant frequencies is also influenced by male body size. Physiologically, the dominant frequencies loons produce are likely influenced by the anatomy of their vocal tracts, as such frequencies are largely affected by the size and

shape of the syrinx, trachea, mouth, and/or bill (Gaunt and Gaunt 1985; Fletcher and Tarnopolsky 1999) that in turn are positively correlated with body size (Wallschläger 1980; but also see Handford and Lougheed 1991; Fitch and Hauser 2002). The negative relationship between dominant frequency, body size, and mass has been observed both within (Bretagnolle 1989; Podos 2001; ten Cate *et al.* 2002) and across (Wallschläger 1980; Tubaro and Mahler 1998; Bertelli and Tubaro 2002) bird species. Therefore, it is not unreasonable to conclude that variation in dominant frequencies of the yodel can be ascribed to variation in male body size and/ or mass. Evolutionary explanations of why males yodel at these dominant frequencies may be better investigated by considering the selective factors responsible for shaping optimal body size.

Clinal geographic character variation often reflects adaptive responses of individuals to changing environmental pressures (Zink and Remsen 1986). Of species like loons that exhibit ecogeographic variability in body size that do not adhere to, or even contradict Bergmann's Rule, selective forces other than those associated with thermoregulation are likely to be important in shaping optimal body size (Mayr 1956). Large body size appears to provide fitness benefits in that larger loons experience greater resource holding power (Piper *et al.* 2000); however, large body size also may incur substantial costs. Such costs may be associated with the physiological costs of flying. Because physical adaptations that enhance underwater foraging also increase the physiological costs to become and remain airborne (Storer 1958; McIntyre 1988), Common Loons have one of the highest wing-loading ratios of any flying bird (Welty and Baptista 1988). To compensate, loons have wings adapted for high-speed flight (Storer 1958), take advantage of prevailing surface winds to become airborne (McIntyre 1988), and utilize air currents to minimize the time and energy spent migrating (Kerlinger 1982; Alerstam and Lindström 1990).

Migration costs may be quite influential in optimizing avian body size (Blem 1975) and wing shape (Mulvhill and Chandler 1990; Lockwood *et al.* 1998; Egbert and Belthoff 2003; O'Hara *et al.* 2006). Such costs are likely to be much higher for loons that migrate longer distances. Individuals breeding in northern Wisconsin or Minnesota that migrate to the Gulf Coast (McIntyre 1988; Belant *et al.* 1991; Evers *et al.* 2000; Kenow *et al.* 2002) travel much farther than individuals that migrate from New Hampshire to the Maine coast (Adams *et al.*, unpub.data). Mid-continental breeders compensate wing-loading limitations by either decreasing body weight, and/or by increasing wing aspect ratio and surface area (Savile 1957), which may, in turn, explain macrogeographic variation in loon body size (also see discussion by Evers 2007).

Consequently, perhaps optimal body size in Common Loons reflects two opposing selective pressures. Because large body size enhances a loon's fighting ability, intrasexual competition favors larger body sizes; however, because smaller body size reduces the physiological costs of migration, selection should also favor smaller individuals at more interior longitudes. Such selective pressures, in turn, likely influence the dominant frequencies these birds produce, and further necessitate studies that examine the function of this interesting territorial signal.

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