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Changing territories, changing tunes: male loons, *Gavia immer*, change their vocalizations when they change territories

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Male common loons produce a territorial vocalization called the yodel. Each male loon has a characteristic yodel that is stable from year to year and differs from that of other male loons on other lakes. Of 13 male loons whose yodels we recorded before and after they changed territories, 12 substantially changed their yodels either the first or second year on the new territory. Furthermore, this change increased the difference between the new resident's yodel and that of the previous resident. This result implies that loons not only change their vocalizations as the birds change territory, but also that the new owner is familiar with the yodel of the resident that it replaces.

The advertising song of birds codes both species and individual recognition (Falls 1982). These two functions compete. Individual recognition of mates, kin and competitors (Catchpole & Slater 1995) requires variability, but species recognition should select for constancy. Evaluation of whether calls, like those of the common loon, permit individual recognition from year to year requires study over long periods. Such studies might also illuminate the trade-off between the constancy required for species recognition and the variability needed for individual recognition. An increasing number of banded common loons whose vocalizations have been recorded has now made such a study possible.

A study of individual recognition in loons is of interest both on theoretical and practical grounds. Some highly endangered birds have loud and conspicuous vocalizations, so a number of investigators have proposed using these vocalizations for individual recognition. By recognizing individuals, it should be possible to estimate population size (McGregor et al. 2000). This approach is attractive because it avoids the necessity of capturing and individually marking individuals. McGregor & Byle (1992) used recordings of European bitterns, *Botaurus stellaris*, to recognize individual bitterns. Peake et al. (1998) examined individuality in the vocalizations of the corn crake, *Crex crex*, and Gilbert et al. (1994) measured the vocalizations of both European bitterns and Arctic loons, *Gavia arctica*. In all of these studies, the investigators could recognize individual birds by their vocalizations and found that they were constant within a breeding season and, for a small sample, from one breeding season to the next. However, none of these studies measured the stability of the vocalizations of marked individuals over several years. We report the results of such a study here.

The yodel vocalization of the common loon is a structurally complex territorial call (Fig. 1) given in response to an intruding adult on, or flying over, a breeding territory. Loons often yodel at night (McIntyre 1988). Study of yodels of marked males (Walcott et al. 1999; Walcott & Evers 2000) has confirmed earlier reports that each male's yodel is distinctive (Barklow 1979; McIntyre 1988; Miller 1988; Vogel 1995). However, Walcott & Evers (2000) reported that four of the male loons they studied changed territories and, subsequently, changed their yodels. In this paper, we describe changes that took place in the yodels of 13 male loons that switched territories.

First, we assessed the stability of the yodel of a male loon on the same territory from one year to the next. Second, we compared the year-to-year variation in the yodel of the same loon on the same lake to the differences between different loons on different lakes.

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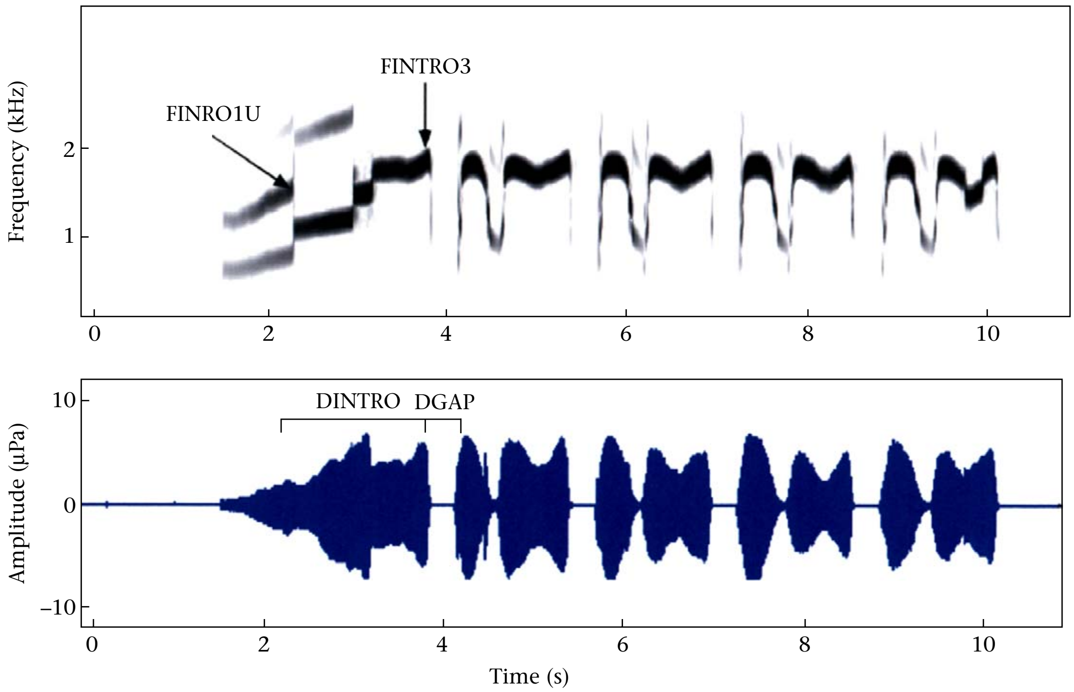

Figure 1. A sound spectrogram and an amplitude display of a loon yodel showing the four features of the introductory phrase that were measured (FINTRO1U, DINTRO, DGAP, FINTRO3) and the four repeat phrases.

Third, we examined how frequently male loons that change territories also change their yodel. Fourth, we compared the magnitude of this change to both the normal yearly change in the same loon and in a control group of loons and compared the magnitude of the change to the magnitude of the difference in yodels of different loons on different lakes. Finally, we considered why male loons change yodels when they change territories.

METHODS

Study Species and Study Site

Common loons are migrants that maintain breeding territories on freshwater lakes to which they generally return each year. In our study areas, the yearly return rate is roughly 80% (Piper et al. 2000a).

We recorded 527 yodels of 16 male loons on 21 artificial lakes (11–364 ha), on the pools at the Seney National Wildlife Refuge near Seney, Michigan, U.S.A. (46°16′N, 86°6′W) and 3107 yodels from 82 loons in 63 lakes (4–150 ha) near Rhinelander, Wisconsin, U.S.A. (45°42′N, 089°37′W). All loons used in this study were banded with standard U.S. Fish and Wildlife Service bands and three coloured leg bands. All recordings used were made from these banded, known individuals. In both populations, loons have been studied and their yodels recorded for 4–12 years.

Eliciting and Recording Yodels

Five or more yodels were elicited from each male by playing recordings of loon vocalizations as described in Walcott et al. (1999). We recorded yodels with portable DAT or Marantz cassette recorders equipped with Sennheiser MKH-70 shotgun microphones.

Measurements and Data Analysis

We made four measurements from each recorded yodel using the Canary V1.5 sound analysis software package (Charif et al. 1995; Fig. 1): DINTRO, the duration of the last two notes of the three-note introductory syllable; DGAP, the duration of the gap between the introduction and first repeat syllable; FINTRO1U, the peak frequency of the end of the first note of the introduction; FINTRO3, the peak frequency of the last note of the introduction. Walcott et al. (1999) showed that these four features were sufficient to distinguish the yodels of different loons from the Seney population using discriminant analysis.

We used canonical discriminant analysis (SAS 1988) to generate four canonical variables that are ranked in order of their ability to explain between-loon variation in the four measured features (Walcott et al. 1999). This procedure was applied separately to all Seney and Wisconsin yodels, resulting in four canonical variables for each yodel. Thus, even though the sample size for any one loon in one year may be low, the discriminant analysis is based on the entire Seney or Wisconsin population. This provides a yodel-to-variables ratio that greatly exceeds the 20 samples per variable recommended by Stevens (1996).

Over the years of this study, we recorded yodels from 13 male loons that switched territories; two of these switched twice. We compared the change in their yodels after the switch with the normal, year-to-year change either before or after the change in territory. Thus each loon served as its own 'control'. A second approach was to compare the change in the yodel after the switch with the normal, year-to-year yodel change of a control group of loons. To provide a random sample of yodels for comparison, we selected yodels from loons on other lakes whose names were at the beginning of the alphabet. We selected the first 18 lakes, five from Seney and 13 from Wisconsin, where there were a minimum of five yodels per year for at least 2 years. Loons in this paper are referred to by their U.S. Fish and Wildlife band number to avoid ambiguity.

The Constancy of Yodels

To assess the within-year variability in yodels for each individual, we calculated the standard deviation of the means of the first two canonical variables for each loon in each year on each control lake. We then pooled all the loons' yodels for all years on each lake and repeated the measurement, which gave us an index of the overall variability of yodels from a given loon on the same lake over several years. Finally, to estimate total variability in yodels within Michigan and Wisconsin populations, we measured the standard deviation of the mean of each of the two canonical variables for all loons on control lakes.

Although standard deviations give an index of the variability of the yodels in canonical space, there could be an overall movement of the whole yodel cluster in canonical space from one year to the next. This would mean that there was a systematic shift in some feature(s) of the yodel. A difference in the value of the mean of each of the canonical variables from one year to the next would be a measure of such a shift. Territorial change often takes place between years, so we measured the amount of movement from year to year for a loon remaining on the same lake. Using the sample of 18 control lakes, we calculated the mean for each canonical variable for each year. We then subtracted the mean for the following year to calculate distance between the two means. These differences were then squared and summed and the square root taken to give the Euclidean distance between the centroids of the two yodel clusters. To gauge the difference between the yodels of different loons on different lakes, we calculated the mean for each of the four canonical variables for each loon on the control lakes. We then measured the distance between the centroids of the yodels for every combination of loons within the Seney and the Wisconsin populations separately. These individual distances for both Seney and Wisconsin loons were then averaged to find the mean distance between different loons.

Territory Switching

To test the null hypothesis that the yodels of an individual are stable between years, we examined a critical prediction that yodels should not change more for individuals that change territories than for individuals remaining on the same territory. Thus, we measured the differences in the mean canonical variables of the yodels from loons between their old and their new lakes. For those loons whose yodels changed, we examined which measured feature(s) of the changed yodel led to the difference. We compared the magnitude of the changes in the yodel to the normal, between-year changes in the yodel from the same loon on the same lake and to the differences between different loons on different lakes. Whether the change in yodel might be associated with the change of the territorial female was determined by looking at those pairs in which there was a switch in female but not the male. We measured the magnitude of yodel change in the years before and after the female switch. Finally, to determine whether the evicting male imitated the yodel of the previous male on the territory, we compared the distance between each usurping male's yodel and that of the former resident both before and after the territory switch. A male that was imitating the previous male should change its yodel to decrease the distance between its yodel and that of the previous resident. The same approach was used to evaluate whether the change in yodel increased or decreased its similarity to that of the yodel from the new male's nearest neighbour on an adjacent lake.

RESULTS

Constancy of the Yodel

We plotted canonical variables (cv) 1 versus 2 (Fig. 2a) and cv 1 versus 3 (Fig. 2b) from yodels from the same individuals that resided on the same territories on the first five Wisconsin control lakes. Although there was some within-individual variability in yodels, there was little overlap between these different birds' yodels. The mean standard deviation of the first canonical variable varied from 0.38 to 1.41 in a single year (grand mean $\pm$ SD $= 0.68 \pm 0.24$). However, pooling all the yodels for the same loon for all years increased the standard deviation for cv 1 from 0.68 ± 0.24 to 0.89 ± 0.32 and that for cv 2 from 0.54 ± 0.26 to 0.77 ± 0.51 (Table 1). Pooling all the yodels from Seney, the mean of cv 1 increased to 1.95 and the mean of cv 2 increased to 1.37; for all the Wisconsin Lakes, the mean of cv 1 was 1.89 and that for cv 2 was 1.51. It is not surprising that variability increased as more loon yodels were included, but this more inclusive measure puts the variability of individual loons in the same lake during the same year in perspective. Although the standard deviation of the canonical factors gives one measure of variability, it does not address whether a loon's yodel changes. A systematic change in any of the measurements that we made should result in a movement of the yodel in canonical space.

Yodel Change from Year to Year

To examine the year-to-year changes in the yodel of the same loon on the same lake, we measured the difference in the position of the centre of the cluster of yodels plotted in canonical space, between years. Table 2 presents a year-by-year analysis for 18 loons that did not change territories. There clearly was a change in the yodel measurements and, hence the canonical variables, that led to a movement of the yodels in canonical space (canonical units per year range 0.15–2.40; $\overline{X} \pm \text{SD} = 1.12 \pm 0.30$).

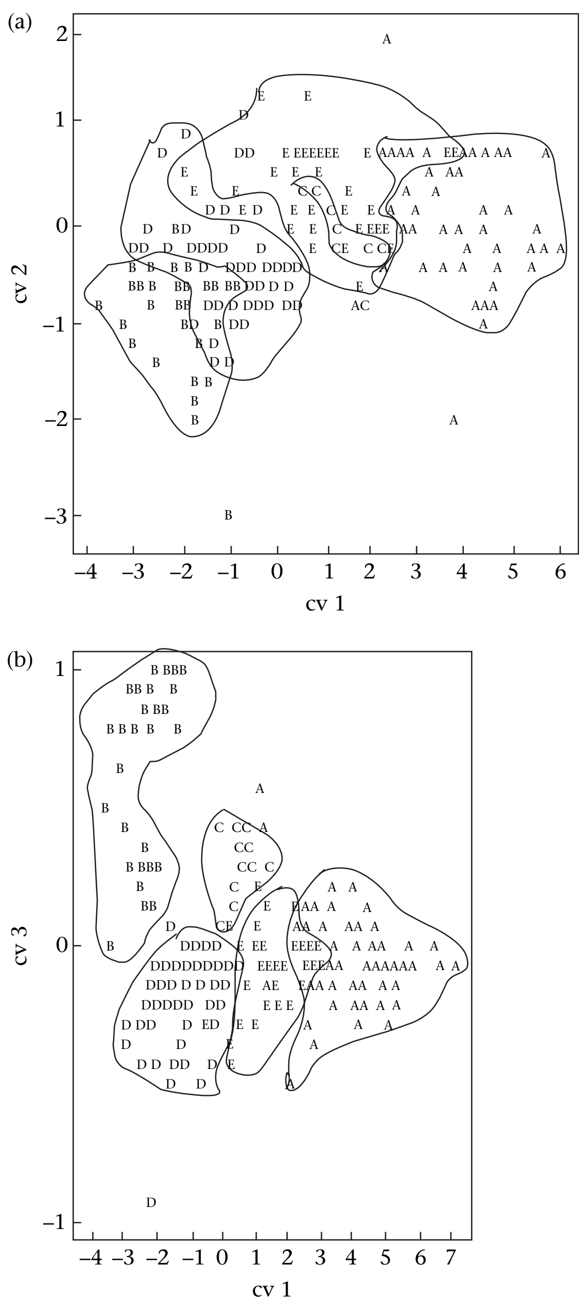

Figure 2. (a) The yodels of the first five Wisconsin control loons plotted in canonical space. In this case, canonical variable (cv) 1 is plotted against cv 2. The letters represent the different loons with all years pooled. Circles enclose the majority of the data points to draw attention to the differences. The five lakes and corresponding loons are: A = Alva, 838-147-47; B = Bear, 958-845-32; D = Brown, 628-227-05; E = Burrows, 848-033-89; C = Curry, 958-845-18. (b) The same loon yodels as in (a) but cv 3 is plotted against cv 1. The yodels of some loons are better separated by this plot, others by the previous one.

This movement of the yodel cluster in canonical space was significantly greater than the average standard deviation of the scatter of the individual yodels in any single year (paired *t* test, two tailed: $t_{18} = -4.627$, $P = 0.0002$; $\overline{X} \pm SD = 0.68 \pm 0.24$) or even with all years pooled (paired *t* test, two tailed: $t_{18} = -2.279$, $P = 0.0358$).

Yodels from Males that Changed Territories

Thirteen male loons changed territories where we recorded yodels both before and after the change. When the loons changed from one territory to another, the mean ± SD distance that the centroid of the canonical variables moved was 3.37 ± 2.97 canonical units (Table 3). For 10 of these 13 loons, we have recordings from years when they did not change territories. Between these years, there was a mean ± SD yodel change of 1.20 ± 0.55 units. The difference between the change in each loon's yodel in years when it maintained the same territory and when it switched was significant (paired *t* test, two tailed, unequal variance: $t_{10} = -2.647$, $P = 0.027$). The yodel for most loons was stable both before and after the change (Table 3, Fig. 3).

In a second comparison between yodels from loons that changed territory and yodels from control loons, which did not switch territories, the nonswitchers differed from the switchers in the years that they changed territories ($\overline{X} \pm SD = 1.12 \pm 0.30$; Student's *t* test, two tailed, unequal variance: $t_{14} = 3.562$, $P = 0.0057$) but not from those years in which the same loon remained on the same lake ($\overline{X} \pm SD = 1.20 \pm 0.55$; $t_{11} = 0.119$, $P = 0.9073$).

For loon 848-507-41 that moved from Dorothy to Hodstradt, the change in its yodel on the same lake (1.91 canonical units) was greater than the difference when it changed lakes (1.49; Table 3). This loon was displaced from Hodstradt after one year, so we could not assess his yodels in the years following his territory switch. Another loon, 838-145-03, moved from Bird to Little Carr. When this loon moved to an adjoining lake, Big Carr, the following year, its yodel changed by 11.06 canonical units (Table 3). Furthermore, loon 848-033-66 moved from Long Lake to Sand, then moved back to Long in the following year, and its yodel changed by 2.76 canonical units, moving back to what it had been previously on Long Lake (Table 3). Neither of these second moves is included in the statistics. There are two other examples of loons whose yodels were recorded on other lakes. The Birch Lake male (838-147-25) also defended Muskie as a multilake territory, and the difference between its yodel on the two territories was 1.85 canonical units (Table 3). Second, the Shallow male (848-046-04) intruded on Tom Doyle but did not breed there, and the difference in its yodel from Shallow to Tom Doyle was 1.11 canonical units (Table 3). These temporary changes in lake had no measurable effect on these loons' yodels.

Thus, some feature of the yodel must change as these males change territory. Table 4 summarizes the change in each of the four measurements of the yodel. There was no obvious or consistent pattern to this change. Some loons changed their yodel's frequency; others changed the timing.

Different Loons on Different Territories

To evaluate the change in each loon's yodel with a change in territory, we compared this change with the normal difference between different loons. For the 18

Table 1. For all the yodels from loons on the control lakes, the mean of the standard deviation of canonical variables (cv) 1 and 2 calculated yearly and for all years pooled

				Mean SD			
				Each year, each lake		All years pooled	
Loon	Lake	N	Years	cv 1	cv 2	cv 1	cv 2
0838-147-61	A-Pool	39	8	0.52	0.23	0.87	0.48
848-506-44	A2-Pool	21	3	0.65	0.50	1.02	0.95
888-160-19	C2-Pool	20	3	0.70	0.73	0.85	0.88
618-111-18	D-Pool	52	9	0.41	0.37	0.73	0.65
848-507-47	G-Pool	27	4	0.65	0.29	0.83	0.48
838-147-47	Alva	56	5	0.96	0.41	0.97	0.10
958-845-32	Bear	37	3	0.62	0.51	0.66	0.73
628-227-05	Brown	61	7	0.39	0.50	0.70	0.58
848-033-89	Burrows	44	4	0.86	0.38	1.05	0.44
958-845-18	Curry	47	3	0.70	0.78	0.80	0.78
848-507-41	Dorothy	36	3	0.60	0.71	0.83	0.95
848-046-67	Emma	62	6	1.41	1.28	2.03	2.61
838-150-22	Flannery	40	4	0.85	0.39	1.12	0.71
848-507-38	Gross	82	5	0.66	0.82	0.87	0.94
888-161-14	Langley	79	4	0.38	0.71	0.54	0.84
888-161-18	Little Bearskin	41	6	0.50	0.31	0.66	0.65
618-111-54	Lumen	87	7	0.65	0.33	0.62	0.66
848-045-42	Long-2	47	5	0.64	0.42	0.78	0.46
$\overline{X} \pm$ SD				0.68±0.24	0.54±0.26	0.89±0.32	0.77±0.51

loons on the control lakes (88 comparisons), the mean $\pm$ SD difference between their yodels was 2.49 ± 1.34 canonical units. There was no significant difference between the magnitude of the change in the yodels of loons that switched territories and the yodels of different loons on different territories when all the years were pooled (Student's t test, two tailed, unequal variance: $t_{15} = 1.564$, $P = 0.1388$). However, the lake-to-lake or loon-to-loon difference was greater than the average yearly change for any individual loon on the control lakes within any one year, or even from one year to the next (Student's t test, two tailed, unequal variance: $t_{103} = 8.617$, $P \leq 0.0001$). Furthermore, the magnitude of the annual change in the yodels of loons that switched territories between years but remained on the same lake ($\overline{X} \pm \text{SD} = 1.20 \pm 0.55$) was significantly lower than the difference in yodels between different loons on different lakes ($\overline{X} \pm \text{SD} = 2.49 \pm 1.34$; Student's t test, two tailed, unequal variance: $t_{95} = 6.947$, $P \leq 0.0001$). Thus when loons switched lakes, the magnitude of their yodel shift was equivalent to that of a different loon.

Although the average annual change in the yodel of the same loon on the same lake was roughly one canonical unit, over a period of years, the direction of the change was erratic. The result was that an individual loon's yodel remained within a small area of canonical space (Fig. 4). In contrast, changes in yodels that accompanied territory switching were directional and stable across years ($N = 6$ loons).

Male loons change territories either because they have been evicted by an intruder, because they themselves evict a resident or because they settle within a vacant territory (Piper et al. 2000b). Based on the number of chicks fledged over a 9-year period as one index of lake territory quality, 10 of the 13 loons moved to lower-quality territories, but only three moved to better territories.

The change in male yodels may also be related to the change in female that comes with the new territory. On eight occasions, a new female took over a territory where we had recordings from the resident male both before and after the female take-over ($\overline{X} \pm \text{SD} = 1.20 \pm 0.53$ canonical units; annual change for years with no take-over for these same loons was 1.08 ± 0.42). This difference was not significant (Student's t test, two tailed, equal variances: $t_{15} = 1.719$, $P = 0.1062$). The second year after the female take-over, the mean $\pm$ SD change in yodels was 1.04 ± 0.362 canonical units, which also did not differ significantly from the change in yodel in years without a female take-over (Student's t test, two tailed, equal variance: $t_{11} = 1.850$, $P = 0.0914$).

Males may also change their yodels to maximize differences between their yodels and those of their new neighbours. We have data for eight loons that moved and for their closest neighbour. In two of these, the yodels of the switching male became similar to those of his new neighbour and in five the difference increased. There was no significant difference between the yodel of the switching male and that of his nearest neighbour before and after the switch ($\overline{X} \pm \text{SD} = 0.75 \pm 1.98$ units; Student's t test, paired, two tailed: $t_{13} = -1.362$, $P = 0.1982$).

Finally, the change in yodel might be related to the yodel of the previous male on the territory. There are three possibilities: the intruder could mimic the yodel of the previous male, he might make his yodel as different as possible to signal a new loon on the territory, or he might, as with the relationship to his nearest neighbour, make a change to his yodel that has no relation to that of the previous territorial male. To evaluate these three possibilities, we compared the intruder's yodel both before and after the territorial take-over with that of the previous

Table 2. Control lakes with the yearly change in the yodels from loons that did not change territories

Loon/lake	Year	*N*	Distance	Lake mean
Seney, Michigan				
848-506-44				
A2 East	1999	2		
	2002	11	1.36	
	2003	7	1.62	1.49
838-147-61				
A-Pool	1996	5		
	1997	2	2.14	
	1998	5	1.38	
	1999	5	0.42	
	2000	4	2.40	
	2001	2	1.07	
	2002	5	1.44	
	2003	11	1.15	1.43
618-111-18				
D-Pool	1990	5		
	1992	10	1.08	
	1993	3	1.30	
	1994	7	2.13	
	1995	4	2.34	
	1996	6	1.92	
	1997	5	1.53	
	1998	5	2.12	
	1999	6	0.89	1.66
845-507-47				
G-Pool	1990	5		
	1994	7	1.15	
	1997	5	1.47	
	1998	9	0.83	1.15
888-160-19				
C-2 Pool	1999	6		
	2000	3	2.13	
	2003	11	0.53	1.33
Wisconsin				
838-147-47				
Alva	2000	8		
	2001	16	1.73	
	2002	9	1.15	
	2003	10	0.63	
	2004	13	0.69	1.05
848-507-41				
Dorothy	1999	7		
	2000	14	1.29	1.29
628-227-05				
Brown	1998	2		
	1999	4	0.73	
	2000	7	0.86	
	2001	9	0.86	
	2002	10	0.62	
	2003	15	0.23	
	2004	14	1.27	0.76
848-046-67				
Emma	1998	5		
	2000	7	0.94	
	2001	17	1.09	
	2002	10	1.68	
	2003	10	1.06	
	2004	13	0.52	1.06
958-845-32				
Bear	2002	12		
	2003	15	0.37	
	2004	10	1.44	0.90
848-033-89				
Burrows	2000	6		
	2001	13	1.08	
	2003	10	1.57	
	2004	15	0.19	0.95
958-845-18				
Curry	2002	18		
	2003	18	0.31	
	2004	11	0.41	0.36
838-150-22				
Flannery	2000	12		
	2001	11	1.45	
	2004	7	0.93	1.19
848-507-38				
Gross	2000	8		
	2001	16	0.59	
	2002	23	0.84	
	2003	10	0.91	
	2004	25	1.53	0.97
888-161-14				
Langley	2000	7		
	2001	34	1.22	
	2002	19	0.69	
	2003	19	0.87	0.93
888-161-18				
Little Bearskin	1997	6		
	1998	3	0.98	
	1999	2	0.81	
	2000	13	1.28	
	2001	8	1.09	1.04
618-111-54				
Lumen	1997	2		
	1998	4	1.67	
	1999	2	0.86	
	2000	17	2.17	
	2001	24	0.34	
	2002	23	0.95	
	2003	15	1.02	1.17
848-045-42				
Long-2	1998	4		
	2000	7	1.44	
	2001	5	1.62	
	2002	21	0.74	
	2003	10	1.67	1.36
				$\overline{X} \pm SD = 1.12 \pm 0.30$

territory holder. We have nine instances with samples of three yodels or more from the previous territory holder and from the intruder both before and after his take-over of the territory. In all nine cases, the intruder significantly increased the difference between his yodel and that of the previous resident male ($\overline{X} \pm SD = 0.59 \pm 0.46$ canonical units; Student's t test, paired, two tailed: $t_9 = 3.813$, $P = 0.005$; the direction of change was also significant; sign test: $P = 0.02$; Table 5).

DISCUSSION

The Yodel

The male loon's yodel consists of two parts, a group of introductory phrases followed by a highly variable

Table 3. Loons that changed lakes and the canonical distance that their yodels changed

Loon/lake, year	*N* yodels	Canonical distance
848-047-58		
C2-Pool 1998	2	
H-Pool 1999	7	3.99*
838-147-66		
E-Pool 1992	5	
E-Pool 1993	10	0.49
E-Pool 1994	11	0.67
E-Pool 1997	6	1.18
J-Pool 1998	5	1.09
J-Pool 1999	6	3.16*
758-781-78		
T2W 1993	6	
B-Pool 1996	13	0.47
B-Pool 1997	5	3.29*
B-Pool 1998	7	1.31
B-Pool 1999	7	1.73
B-Pool 2000	5	1.28
B-Pool 2002	13	1.03
B-Pool 2003	18	2.17
758-781-02		
B-Pool 1990	3	
B-Pool 1992	6	0.59
B-Pool 1993	3	0.67
B-Pool 1994	9	0.88
B-Pool N 1996	13	2.03*
B-Pool N 1997	3	0.85
838-150-21		
Langley 1997	5	
Loon 2001	10	2.60*
Loon 2002	8	1.35
Loon 2003	5	0.96
838-145-03		
Bird 1997	5	
Little Carr 1999	2	10.89*
Big Carr 2000	5	11.06*
Little Carr 2001	5	2.51
Big Carr 2002	4	2.00
Little Carr 2002	2	2.43
838-145-61		
Long 1997	6	
Long 1998	2	0.61
Fawn 1999	4	0.89*
838-147-33		
Hemlock 1997	8	
Clear 2001	5	5.60*
Clear 2003	16	2.04
Clear 2004	14	0.70
848-507-41		
Dorothy 1999	7	
Dorothy 2000	14	1.91
Hodstradt 2001	14	1.49*
848-046-16		
Bearskin 2000	9	
Bearskin 2001	8	0.69
East Mitchell 2002	4	1.09*
East Mitchell 2003	6	0.78
848-033-66		
Long Lake 2000	6	
Long Lake 2001	7	1.30
Sand Lake 2002	11	2.68*
Long Lake 2003	17	2.76*
Long Lake 2004	18	0.57

Table 3 (*continued*)

Loon/lake, year	*N* yodels	Canonical distance
848-048-10		
West Horsehead 2000	7	
East Horsehead 2002	5	1.24*
628-227-05		
Two Sisters 2003	9	
Brown 2004	10	4.18*
838-147-25 (multilake territory)		
Birch 1998	4	
Birch 1999	4	1.85
Muskie 1999	8	1.57
Muskie 2000	6	1.63
848-046-04 (intrusion)		
Shallow 1998	3	
Tom Doyle 2000	7	1.11
Shallow 2000	6	1.31
Shallow 2001	9	2.37
Shallow 2002	7	0.49
Shallow 2003	30	0.67
Shallow 2004	17	0.61

*Indicates year that yodel changed.

number of repeat phrases. Walcott et al. (1999) reported that four loons from the Seney population could be categorized correctly using four measurements of the introductory phrase. In a more extensive study of 73 yodels from 16 different Wisconsin loons, Lindsay (2002) found that discriminant analysis successfully classified 78% of the yodels, but only when measurements from both the introduction and the repeat syllables were used. Using the four introductory measures alone resulted in correctly

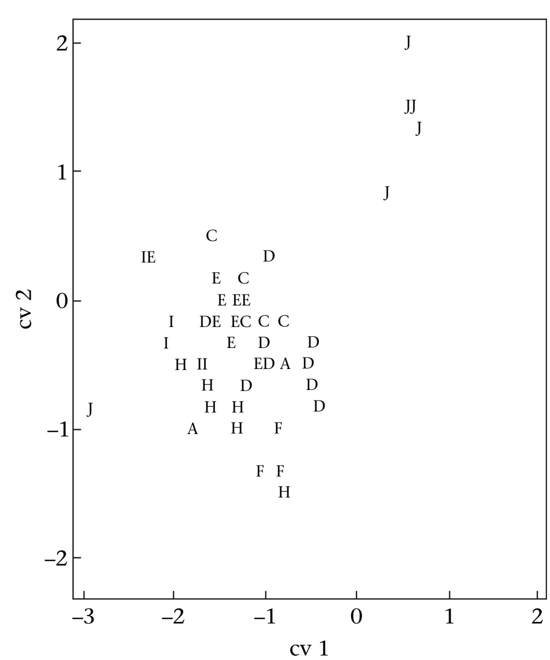

Figure 3. The yodels of the E-Pool loon plotted by year. 'A': yodels recorded in 1990; 'B–J': yodels recorded in 1991–1999. This loon moved from E-Pool to J-Pool in 1998 (I) and changed its yodel in 1999 (J).

Table 4. The change in mean yodel measurements that followed a change in territory (significance is based on a Student's *t* test, with unequal variances)

Loon	Lake to lake (number of yodels)	DINTRO (ms)	DGAP (ms)	FINTRO1U (Hz)	FINTRO3 (Hz)
848-047-58	C2 Pool (2) to H-Pool (7)	+309*	+49***	+84***	+100
838-147-66	E-Pool (37) to J-Pool (6)	+237*	−14	−135***	+231*
758-781-78	T2W (6) to B-Pool (5)	+67	+16*	+51	+352***
758-781-02	B-Pool (23) to B-Pool North (13)	−131	+51***	+32	−38
838-150-21	Langley (5) to Loon (10)	+12	−62***	+135***	+72***
838-145-03	Bird (5) to Little Carr (2)	−113	−46*	+983*	+608***
838-145-03	Little Carr (2) to Big Carr (5)	+513**	+12	−1040**	−220***
838-147-33	Hemlock (8) to Clear (5)	−230***	−106***	−85	+193***
838-145-61	Long (8) to Fawn (4)	+97	−10	− 63	−34
848-507-41	Dorothy (14) to Hodstradt (14)	+99**	−30***	+41	−6
848-046-16	Bearskin (8) to East Mitchell (4)	−52	+22**	−64*	−26
848-033-66	Long (4) to Sand Lake (11)	−86***	+38***	+21*	−87*
848-048-10	West (7) to East Horseheads (5)	−97	+10	−7	−67*
628-227-05	Two Sisters (9) to Brown (10)	−177***	+46***	−244***	−161***

+: Increase in measurement; −: decrease in measurement.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

classifying only 52% of the yodels. Despite this finding, we used these four measures of the introductory phrase because they distinguished between individuals in both the Seney and Wisconsin populations. Furthermore, the peak frequency of the last introductory note (FINTRO3) was significantly correlated with the dominant frequency of the repeat syllables (Pearson correlation: $r_{158} = 0.636$, $P = 0.0001$), and the duration of the gap between the introduction and the first repeat syllable (DGAP) was also significantly correlated with the duration of the gaps between subsequent repeat syllables ($r_{153} = 0.906$, $P = 0.0001$). Thus, the four measures of the introductory phrase that we used capture some of the information in the repeat syllables. Although the intensity of the end of the first note of the introduction, where FINTRO1U was measured, was less than that of the second and third introductory notes or of the repeat syllables, the end of the second introductory note was comparable in intensity to that of the third note and the repeat syllables. Listening to a loon at longer distances, one hears the frequency and the rough patterning of the introduction and repeat syllables. In close encounters with intruders, however, many of the subtle features of the yodel, like the softer parts of the introduction or the frequency modulation of the repeat syllables, might be important for individual recognition. Thus, the analysis of the repeat phrases of the yodel and our understanding of the temporal variation in the yodel, both within and between individuals, awaits further study.

Whatever the failings of using these four measures of the introductory notes of the yodel, they provide a uniform treatment for all yodels. Thus, if male loons change their yodels as they switch territories, this change should be reflected in these measures.

Constancy of the Yodel

Yodels of individual males showed some variation in the four measures that we considered. It seems intuitively reasonable that as we increase the time span of the measurements, variability should increase. The year-to-year variation was greater than that within a single year, but variability in any one loon's yodels was less than the difference between different loons on different territories. If a male's yodel is specific to that individual loon and differs from all others in the population, this is just the result we would expect. Previous studies (Barklow 1979; Miller 1988; Vogel 1995) have reported that loon yodels are consistent from year to year, but these observations

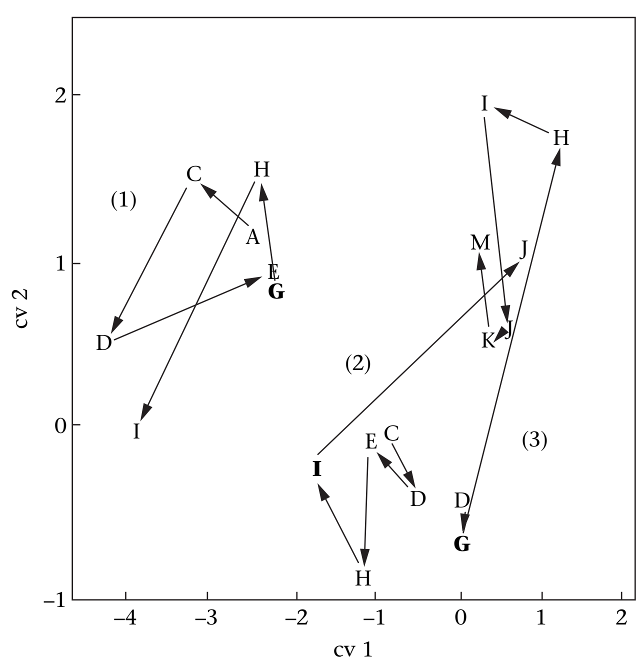

Figure 4. The centroid of each year's cluster of yodels for each of three loons is plotted in canonical space. Numbers refer to individuals: (1) D-Pool loon 618-111-180, plotted for 7 years; (2) E-Pool loon 838-147-66, plotted for 6 years; (3) T2 West-Pool loon 758-781-78, plotted for 7 years. **Bold letters** denote years in which individuals switched territories. Letters refer to the years in which the recordings were made, where A = 1990, B = 1991, and so forth.

Table 5. Change in intruder's yodel relative to the yodel of the previous resident of territory based on the Euclidean distance in canonical units between the yodels of the intruder and the previous resident of the territory before and after the take-over

Loon	Lake to Lake	Distance		
		Before	After	Difference
758-781-78	T2W to B-Pool	2.82	2.88	0.06
758-781-02	B-Pool to B-Pool North	2.45	2.91	0.46
838-150-21	Langley to Loon Lake	3.01	3.65	0.64
838-145-61	Long Lake to Fawn	1.19	1.63	0.44
838-147-33	Hemlock to Clear Lake	0.97	2.51	1.54
848-046-16	Bearskin to East Mitchell Lake	2.25	2.95	0.70
848-033-66	Long Lake to Sand Lake	1.19	1.26	0.07
848-048-10	West Horseheads to East Horseheads	1.27	1.66	0.39
628-227-05	Two Sisters to Brown	2.16	3.17	1.01
			$\overline{X} \pm$ SD change $= 0.59 \pm 0.46$	

were made on unbanded loons, so the identities of the yodeling males could not be confirmed.

Variability in the yodel resulted from a change in one or more of the four parameter(s) that we measured; this is shown as the distance between the centroid of each year's set of yodels as plotted in canonical space. While the annual change was about 1 canonical unit, the difference between different male loons was 2.5 units. This means that the yearly change in any individual loons is small compared to the differences between different loons.

Territory Changes

Twelve of the 13 male loons that changed territories (probably because they either displaced other males or were displaced themselves; reviewed in Piper et al. 2000a, b), changed their yodels. The magnitude of the change was significantly greater than the normal year-to-year variation, and was equal in magnitude to the difference between different loons. This result suggests that loons have considerable flexibility in their vocalizations and are not constrained to a single, fixed yodel.

For some loons that switched territories, the change in vocalization took place immediately after the switch, but for others, the change took place in the year after displacement. Only one male's yodel changed less after he switched territories to a new lake than it did for two consecutive years when he remained on the same lake. The loon with the largest changes, 838-145-03, not only moved the shortest distance in one year, only a few hundred metres from Little Carr to Big Carr, but also had the largest annual change (2.31 units) when he remained on the same territory between years.

One male, 848-033-66, changed its yodel following a territory switch to a new lake, then returned to the old lake and changed his yodel back to approximately what it had been before the switch (2.68 and 2.76 canonical units, respectively). This result suggests that changes in yodels are reversible.

Two males that did not make territory switches but defended (838-147-25) or intruded upon (848-046-04) territories on more than one lake, showed small changes (1.63 and 1.22 units, respectively) in yodels between lakes.

Results of the comparison between changes in yodels in the year of or the year after a territory switch and year-to-year variation on either the new or old territory ($N = 2$ loons for which 4 years of yodels were recorded before their change in territory) suggest that a small annual change in the yodel is followed by a much larger one on the new territory. For six loons for which we had some years of recordings after the shift, the pattern was similar: there was a large change followed by smaller annual changes. This pattern is in contrast to that shown for the control lakes (Table 2). For these lakes, as many as 7 years of recordings showed only small year-to-year variation.

These results argue against the idea that changes in the yodel are simply the consequence of some nonspecific trauma. Such changes would be relatively short-lived and would seem unlikely to persist from year to year. The large yearly changes in the yodel seem only to take place with a change in territory.

We can imagine at least four possible reasons why males change their yodels when they switch territories.

(1) The change in the male's yodel may be related to a change in the female. During a male take-over, the female remains on the territory ($N = 12$) or, during a female take-over, the male remains ($N = 8$). Female take-overs had no effect on the male's yodel, suggesting that it is the change in territory and not the change in female that triggers the male to change its yodel.

(2) A loon that has been forcibly displaced might also change his yodel so that other loons would not recognize his vulnerability. However, if loons attempt to avoid indicating their vulnerability to other male loons by changing their yodels, one would not expect new territorial residents to change their yodels. In fact both displaced males and new territory owners changed their yodels.

(3) A male might change his yodel in such a way as to maximize the difference between his yodel and that of his new neighbours. For about half the loons in our study, yodels of resident males did become increasingly different from their neighbours', but for almost as many others the difference decreased.

(4) An intruder taking over a previous male's territory might change his yodel to imitate that of the male that he displaced, the limited data (nine cases) suggest exactly the opposite; all intruding loons changed their yodels to sound

less like that of the previous territorial male. Thus, the change in yodel does not appear to be a consequence of displacing or being displaced. Rather it appears to be associated with the change in territory itself or intriguingly, perhaps the yodel of the previous resident. This result suggests that the intruding loon must be familiar with the yodel given by the previous territory holder.

A loon taking over a territory could be doing so because, for some reason, the new territory was better than the old, or it could have been forced to move to a less desirable territory. We have no independent measure of territory quality but presumably those territories from which more loon chicks fledge are likely to be 'better' in some sense than territories from which no chicks fledge (Piper et al. 2000b). Comparing changes in the yodel of males that took over 'better' territories that had, over a 9-year period, reared more chicks, to changes in the yodel of birds that moved to 'poorer' territories where fewer chicks had been reared, revealed no obvious differences in the features of the yodel that changed. J. H. Mager (unpublished data) found that FINTRO3 is correlated with the weight of the loon. Assuming that larger males are more likely to displace smaller ones, one could imagine a trend of decreasing FINTRO3 as one loon replaces another. Yet there was no obvious trend in that direction: more than twice as many loons moved to 'poorer' territories than to better territories.

Unfortunately, we do not have long-term productivity records for those loons with changing yodels. The longest record we have is for the T2W male (758-781-78) that took over B-Pool at Seney in 1996. We have recordings from him for the 6 years since he took over his territory. The first year (1996), he retained his old yodel that we recorded on T2W in 1993. The second year he changed his yodel and maintained the change for a few years, and in 2002, he gave yodels that were similar to both his yodel in 1993 as well as to the changed version of his yodel the following year. In fact, there was some intermixing of the two yodel types in each year.

Some loons changed their yodel in the first year that they changed lakes (758-781-02, 838-145-61, 848-046-16, 848-033-66), whereas others changed in the second year (838-147-66, 758-781-78). There is no obvious reason for this difference. In one case where we observed the active displacement of 758-781-02 from B-Pool to B-Pool North by 758-781-78, it was the male that was actively displaced that changed his yodel immediately, while the male that took over his territory changed his yodel in the following year. Loon 838-147-66 changed from E-Pool to J-Pool not because he was evicted by another loon but because the water level in E-Pool was lowered. That loon also changed his yodel in the second year on the new territory. Perhaps loons that take over a new territory change in the second year, whereas loons that are actively displaced by other loons change at once. We simply do not have enough data to decide.

The overall finding is that the yodel of an individual male loon seems to be quite consistent and stable from year to year. If, however, the loon changes territory, it appears to change its yodel. Such a change means that yodels are not likely to be very useful in identifying individual loons if they switch territories. To what extent this might be true of the vocalizations of other birds would seem a ripe prospect for investigation. If a loon taking over a territory changes his yodel to differentiate it from that of the previous male territory holder, and if resident males react with increased vocalizations to the yodels of strangers but much less strongly to yodels of neighbours, as suggested by Lindsay (2002), this could explain the change. Smith (2000) has shown that playing recorded yodels discourages prospective intruders from landing on a territory. It may be that male loons change their yodels to make them unfamiliar to other male loons that are prospecting for territories, which may be a more effective deterrent to a prospecting male loon. This is a hypothesis that can be tested.

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