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Individual variation in song of Black-throated Divers (*Gavia arctica*)

Pekka J. Lehtonen* & Jyrki Lappalainen

*P. Lehtonen, Toppelundintie 5 F 33, FI-02170 Espoo, Finland * Corresponding author's e-mail: pelehtonen@gmail.com*
J. Lappalainen, Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, P.O. Box 65, FI-00014 University of Helsinki, Finland

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The intention of the study was to determine whether male Black-throated Divers (*Gavia arctica*) can be distinguished individually by their vocalization. The songs of 19 male Black-throated Divers (BTDs) were recorded in their territories in the same lake area in 2018–2021 in Finland. The songs were recorded in one year in nine territories and in 2–4 consecutive years in ten territories. The song consists of one introductory phrase and one or more repeat phrases. Seventeen variables were measured from the spectrograms of the introductory phrase and the first repeat phrase. These variables included the frequencies and duration of different parts of the spectrogram. The discriminant analyses were used to examine the recognition of individual BTDs based on the spectral analysis of the male yodels (n = 297) in different territories (n = 19). The discriminant analysis showed that when using 14 of the variables of the yodels, the discriminant analysis classified the yodels to correct territories at a rate of almost 98% based on the cross-validation of all data. This suggests that the same individuals defend their territory from year to year.

1. Introduction

Vocal individuality is useful in situations where visual signals cannot be used, such as in rainforests, meadows with tall grass, or at night (Yee *et al.* 2016, Zsebők *et al.* 2017**,** Chang *et al.* 2018**,** Raymond *et al.* 2020). By recording birds, an assessment of abundance can be made without disturbing the natural behavior of the birds **(**Zsebők *et al.* 2017). Individual recognition of acoustic signals is useful for birds because it enables communication over a longer distance than visual observation (Raymond *et al.* 2020). Vocal discrimination can also be used, for example, for the purposes of a neighbor-stranger discrimination (Vogel 1995, Mager *et al*. 2010, Raymond *et al.* 2020).

Many recent articles have dealt with the individual identification of birds by vocalization. Zsebők *et al.* (2017) explored the individuality of the calls of male Common Cuckoos (*Cuculus canorus*). They conducted a discriminant function analysis on the acoustic variables to distinguish individuals and observed that individuals differ in both the frequency and time of their calls. Discrimination of the male calls of 26 individuals was almost 100% accurate. Budde (2010) analysed the vocal repertoire of the Grey Crowned Crane (*Balearica regulorum gibbericeps*) and showed that individuals and sex identification are possible in the unison call.

Gilbert *et al.* (1994) concluded that spectrograms of the yodel vocalizations of BTDs showed clear qualitative differences between individuals. However, the within-year stability of BTD yodels could not be systemically investigated because of the limited range of recordings. Four BTDs were recorded in the same location in 1991 and 1992 and the spectrograms were very similar. Another *Gavia*-species, Common Loon (*Gavia immer*), has been studied thoroughly and reported to be recognized for their dynamic vocal repertoire (Miller 1988, Vogel 1995, Walcott *et al*. 1999, Mager & Walcott 2007, 2014, Mager *et al*. 2007a, 2012). Walcott *et al.* (1999, 2006) have shown that the male yodel of Common Loon is quite consistent and stable from year to year.

Structural analyses of vocalization (*e.g.*, Barklow 1979, Vogel 1995, Walcott *et al.* 1999) have shown considerable variability among the yodels of territorial Common Loon males. Some elements within the yodel exhibit low intra-individual variability and high inter-individual variability, and territorial loons respond differently to yodels from territorial neighbours and non-neighbours (Vogel 1995, Mager *et al*. 2010). They also change their vocalizations when they change territories to distinguish themselves from the previous owner after taking over the territory (Walcott *et al.* 2006). This suggests that one of the functions of the yodel is to inform others about their identity.

Mager *et al.* (2007a, 2007b) found geographic variation in the body size and vocal behaviour of Common Loons across North America, and that the dominant frequencies of yodels are partly influenced by the body size of males. Mennill (2014) showed that Common Loons called when the abiotic conditions were ideal, *i.e.*, calm weather, no rain, or other distracting noises, for long-range signalling.

Black-throated Diver (BTD) (*Gavia arctica*) is a widely distributed species that breeds on freshwater lakes and ponds in Arctic and Subarctic regions across Eurasia, extending east to the westernmost Alaska (Russell 2020). Individual identification of BTDs is a crucial issue for prioritizing behavioural studies. It can be used to estimate whether the same individuals occupy the same territories from year to year when they return to their territories in spring. Individual identification can also be used to estimate the age of the bird by following them in their territories for long periods of time. Identifying birds individually makes it possible to examine the differences in their social behaviour for example in the company of other BTDs in flocks where social interactions are powerful and versatile. However, visual identification of BTDs during the breeding season is questionable because it can disturb nesting. Therefore, other methods are needed for identification. After the breeding season when visual identification is less disturbing, the summer plumage of BTDs can be used for individual identification (Lehtonen & Lappalainen 2017).

BTDs defend their breeding territories from both conspecific and interspecific intruders (Sjölander 1968, Lehtonen 1970, Eriksson *et al.* 2008). BTDs produce most yodels just after ice break when they have returned to the lake and occupy their territories. At that time, it is possible to hear hundreds of yodels in one day from a single location. In the following weeks, the number of yodels is steady. During breeding, male gives loud, rhythmic, *kuuik-kukuuik-kukuuik…* This territorial call (yodeling) is one of the most well-known features of this species and may under favourable conditions be heard at the distances of 4–6 km (Lehtonen 1970). If the breeding is successful, the BTDs continue regular yodeling till August. In late summer, BTDs are most active after sunset (Lehtonen 1970, Lehtonen & Perämäki 2019).

With a territory song (yodel), male BTDs express their ownership of a certain area and warn other conspecific partners to come to the scene (Lehtonen 1970, Lehtonen & Lappalainen 2017). It is also believed to be a long-range threat signal given during aggressive situations and territorial encounters (Sjölander & Ågren 1972). The song consists of one introductory phrase and one or more repeat phrases (Fig. 1).

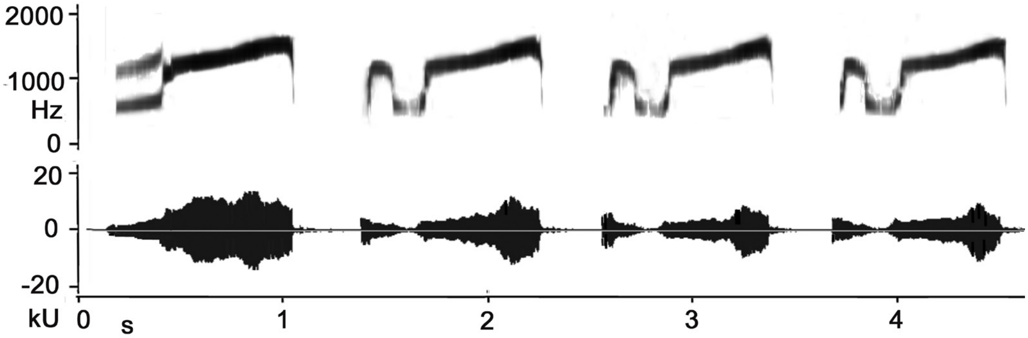

Fig 1. Sound spectrogram (above) showing the change in in frequency (in Hz), and waveform (below) showing the change in energy (kU, kilounits, dimensionless) of a typical yodel over time (in seconds). The yodel consists of an introductory phase of two notes that rise in frequency and repeat phrases of two syllables that follow the introductory phrase.

Lehtonen and Lappalainen (2017) found that individual identification of BTDs can be done based on the details of the breeding plumage. Following that study, one male BTD was photographed regularly over four summers, and based on the plumage, the same male occupied the same territory during the years 2018–2021. However, the use of plumage needs visual observations of the BTDs. In other *Gavia*-species, yodel has been suggested to be used as a tool for identifying different individuals (Walcott *et al.* 1999, 2006). Therefore, here the aim was to examine the territory-specific variation in male BTD yodel based on spectral analysis in order to understand between-individual variation in yodelling in this species. First, the yodel was divided into different, measurable parts and frequencies were measured at certain points of the yodel, and the variability of each of these measurements in each BTDs was compared with the variation of all BTDs (Mager & Walcott 2007). This procedure enables an estimation of the originality of the different parts and frequencies of the yodel and helps to identify which parts of the yodels vary the most. Secondly, these different measured variables of the yodels were analysed in discriminant analysis to estimate if these can be used to identify different BTD males in different territories.

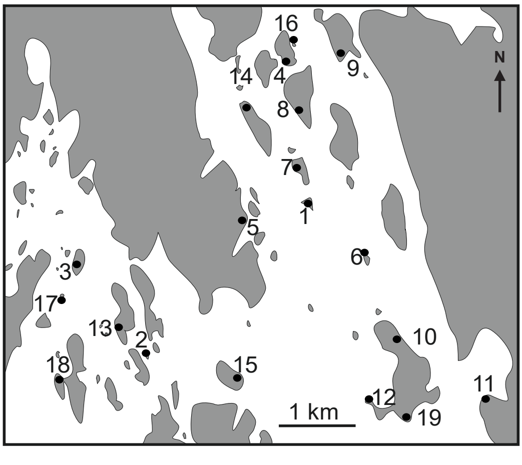

Fig. 2. The study area (Lake Suontee, 61˚39'N, 26˚31'E). The locations of different territories are marked with corresponding numbers, and the sites for recordings with black circles.

2. Material and methods

2.1. Study site and yodel recording

This research was conducted on Lake Suontee (61˚39'N, 26˚31'E) in Finland. Lake Suontee covers an area of 150 km^2 and has 500 islands and islets, supporting about 120 BTD pairs (Virtanen *et al.* 2011, Lehtonen *et al.* 2013, Virtanen 2013, Lehtonen & Lappalainen 2017). The yodels were recorded on 19 territories between May and August in 2018–2021 (Fig. 2). The territories were located within an area of 21 km^2 and were usually 500–1000 meters apart from each other.

The yodels were recorded onto digital memory card using an Audio-Technica AT897 shotgun microphone connected to Zoom H4nPro or to

Zoom H5 hand recorder. The recordings were in 16 bits WAV format. To acquire an adequate sample of yodels from each individual while minimizing disturbance, the recordings were made leaving the recorder as discreetly as possible on the territory of BTDs overnight to perform continuous recording approximately from 7 pm to 7 am. The recording device was installed right next to the water so that the sound would not bounce off the beach terrain but comes directly from the lake to the microphone.

Total recording time was about 1000 hours and about 5000 yodels were recorded. Only recordings made close enough (less than 400 m distance) gave a high-quality spectrum from which all the variables used in the statistical analysis could be measured. High quality spectra were obtained from 297 yodels. Annually 5 to 15 yodels per territory were used for statistical analysis. Playback was not used.

Spectrograms were generated using the Cornell laboratory Raven Pro (version 1.6) bioacoustic analysis software. The frequency (the nearest Hz) and duration (the nearest milliseconds, ms) variables of the introductory phrase and the first repeat phrase of each yodel were measured (Table 1, Fig. 3).

2.2. Statistical analyses

Following previous work by Mager & Walcott (2007), the coefficient of variation (CV) was calculated from different yodel variables first within individuals (CV_i) and then between individuals (CV_b). The CV was calculated as:

$$CV = (s \times 100)/ Y \quad (1)$$

where s is the standard deviation and Y is the arithmetic mean of the data set. The ratio between individuals (CV_b) was compared with the average

Table 1. Definitions of measured and calculated variables of yodels recorded from Black-throated Divers. Duration is in ms, and frequency is in Hz

Variables	Definition
Measured	
DI	Duration of the introductory phrase
DI1	Duration of first note of introductory phrase
DI2	Duration of second note of introductory phrase
DGAP	Duration between introductory and first repeat phrase
DR1	Duration of first repeat phrase
DR11	Duration of first note of first repeat phrase
FI1	Frequency with highest intensity at end of second harmonic of first note of introductory phrase
FI2C	Centre frequency of second note of introductory phrase
FI2B	Frequency of beginning of second note of introductory phrase
FI2E	Highest frequency at the end of introductory phrase
FR11C	Centre frequency of first syllable of first repeat phrase
FR11	Highest frequency of first syllable of first repeat phrase
FR12B	Frequency of beginning of second note of repeat phrase
FR12E	Highest frequency at the end of second note of first repeat phrase
FR12C	Centre frequency of second note of first repeat phrase
Calculated	
FIBE	Difference in frequency during second note of introductory phrase (FI2E minus FI2B)
FR1BE	Difference in frequency during second note of first repeat phrase (FR12E minus FR12B)

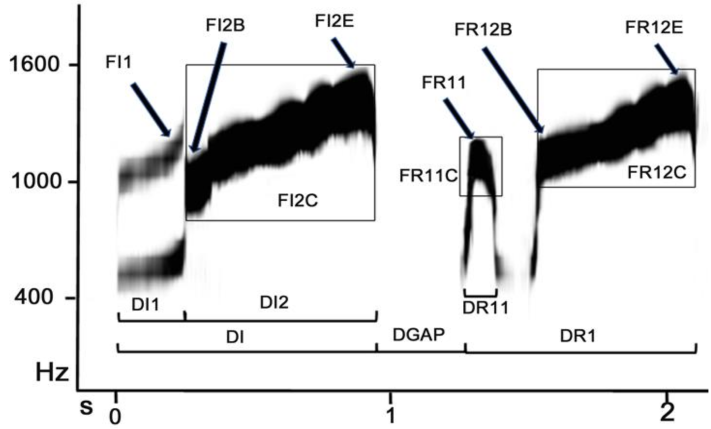

Fig. 3. Sound spectrogram of the introductory phrase and first repeat phrase showing the change in frequency of a typical yodel over time. In x-axis time is in seconds, and in y-axis is the frequency in Hz. Measured variables are explained in Table 1.

CV within individuals (CV_i) as:

$$\text{Ratio} = CV_b/CV_i \qquad (2)$$

to determine those acoustic variables that exhibit a low within-individual variability yet high between-individual variability. These, in turn, could help determine which variables could discriminate individuals.

The identification of male yodel in each territory was done with the discriminant analysis (SAS 2014). First, the best set of measured variables of the yodel were selected using stepwise selection with all the data in the discriminant analysis. The discriminant analysis using stepwise selection of variables removed three variables from the analysis, when all the 17 variables were included. The removed variables were DI2, FIBE and FR12B (see Table 1 for variable definitions). The correlation analysis showed that the variable DI2 was strongly correlated with DI ($r = 0.80$, n = 297), and FIBE with FI2E ($r = 0.96$, n = 297) and FR12B ($r = 0.86$, n = 297). If the stepwise analysis was started excluding the variables DI and F12E, the variable FR12B was still removed. The ASCC values suggested that these two discriminant analyses showed similar potential discriminatory power ($p < 0.0001$, ASCC = 0.424 in both analyses) (SAS 2014).

The best set of selected variables and all the data were then analysed with discriminant analysis using territory as a class. Here, the prior group size probability was used, and the misclassification estimate was based on cross-validation, *i.e.*, the leave-one-out option. The data were also divided into train and test data so that the train data included all territories, but the test data were selected among those territories that had more than one year of data. Because there were some territories that had only one year of yodels, those were put in the train data, and all territories that had data over several years, only the last year was placed in the test data (territories 1, 3–6, and 13–17) (Table 2). Here, both the options in the prior group size effects were compared (no prior group size vs. prior group size).

3. Results

3.1. Structure of the song

In a typical yodeling position, the male head was at a 40 degree angle (± 3 degrees, n = 9, Fig. 4).

Table 2. The number of analysed yodels in different territories during the studied years.

Study year	Territory number	Yodels
2018	1	8
2019	1, 2, 5–7, 17	54
2020	1, 3–6, 8, 13–18	104
2021	1, 3–6, 9–16, 19	131

Structurally, the yodel (*i.e.*, song) is composed of two distinguishing features: an introductory phrase of two notes that rise in frequency, and a series of 2-syllable repeat phrases that follow the introductory phrase (Fig. 1). There are most often 2–4 repeat phrases, but sometimes even 5–10. Depending on the number of repeat phrases the song lasts from two seconds to ten seconds. The duration from beginning of the introductory phrase to the end of the first repeat phrase varied from 1.63 seconds to 2.58 seconds (n = 297).

The duration and frequency of different measured variables in yodels varied considerably (Table 3). Some frequency variables, such as FI1, FI2B, FI2E, FR11, FR12B and FR12E (Table 1 and 3) showed very little within-individual variability (CV_i, Table 3). Some variables, such as DI, DR and FIE exhibited high between-individual variation (CV_b, Table 3). The CV_b/CV_i score of all variables was in the range 2.2–7.0 showing a large difference between CV_i and $CV_{b.}$

In most cases the song of different BTDs is much alike and the identification of the individual in question can be made only by spectral analysis. The easiest way is to look at frequency at the end of introductory phase (FI2E, Table 1, Fig. 3). This frequency is exceptionally stable (CV_i = 1.42) within and between years and gives a rapid information of the bird in question. Although the introductory and the repeat phrases have most often two notes, the frequency (in Hz) of the second note rises abruptly in yodelings of some individuals. If this happens, then the end frequency of the second note (FI2E and FR12E, Table 1) and the difference between the end and start frequency of the second note (FIBE and FR1BE, Table 1) are exceptionally high.

3.2. Discriminant analyses

The stepwise discriminant analysis removed three variables, DI2, FIBE and FR12B, from the analysis, thus including 14 variables (Table 4). The misclassification rate of these 14 variables was 2.02% based on cross-validation in all data. In the analysed data, six different yodels from four different territories were misclassified. Notably, there was misclassification of the yodel from territory 6 into territory 16 and *vice versa*, both recorded in the summer of 2021, and two yodels that were misclassified from the territory 7 into territory 15 both recorded in the summer of 2019. In spite of these, the correct classification was almost 98% in 19 territories and in 297 yodels analysed (Fig. 5).

The manual division of the data into the train (n = 201) and test data (n = 96) showed that the misclassification rate was 16.40% in the test data, when the prior group size probabilities were not considered. From the five yodels recorded in territory 3, three were misclassified into territory 19. The distance between the territories in yodels that were misclassified were in general more than

Fig. 4. Black-throated Diver male in a typical yodeling position.

Table 3. Mean and standard deviation (std) of yodel variables recorded from individual males. CV_i and CV_b are variance variables within-individual and between individual, respectively. Ratio is CV_b/CV_i.

Variables	Mean	Std	Range	CV_i (%)	CV_b (%)	Ratio
Duration (ms)						
DI	965	119	715–1273	3.2	12.3	3.83
DI1	244	72	121–510	9.6	29.6	3.08
DI2	722	83	507–963	4.0	11.5	2.86
DGAP	297	40	200–423	6.0	13.4	2.22
DR1	822	113	572–1095	3.4	13.7	4.04
DR11	113	30	49–214	11.8	27.0	2.27
Frequency (Hz)						
FI1	1337	51	1212–1473	1.77	3.8	2.17
FI2C	1324	136	1034–1809	4.06	10.3	2.53
FI2B	1118	44	1037–1252	2.03	3.9	1.93
FI2E	1677	151	1417–2064	1.42	9.0	6.31
FR11C	1084	57	947–1292	3.12	5.3	1.69
FR11	1230	56	1103–1438	2.08	4.5	2.17
FR12B	1218	49	1059–1333	1.71	4.0	2.34
FR12E	1640	153	1358–2024	1.33	9.3	7.04
FR12C	1340	136	1026–1809	4.41	10.1	2.30
Calculated variables (Hz)						
FIBE	559	146	254–987	5.60	26.2	4.68
FR1BE	421	144	198–813	7.03	34.3	4.87

3 km (mean 3.5 km, range 1–5.5 km). The shortest distance in which the yodel was misclassified was between the territories 13 and 18 (Fig. 2). When the prior group size probabilities were considered, the misclassification rate was 10.46%.

4. Discussion

The obtained results on BTD vocalization suggest, that the BTD males in each territory are the same individuals even in different years. In a similar study, Walcott *et al.* (1999, 2006) ringed individuals of the closely related Common Loon to verify the individual characteristics of the yodeling. In BTDs individuality can be verified by photographing the breeding plumage of BTDs and by examining whether the plumage remains the same from year to year (Lehtonen & Lappalainen 2017) or by ringing the BTDs and recapturing them annually to check their identity. However, the BTD is a highly sensitive species and both methods impose strong disturbance on them, as the former would require photographing the BTDs close enough in nesting time when they are hiding. Photographing requires a long presence in the vicinity of the nest and is not advisable due to interference to nesting. Annual catches near the nest in open waters is extremely difficult and can harm the BTDs. In our view the only safe way to catch the BTDs is during dark nights in August–September while capturing during the breeding season can cause major disturbance for nesting and probably abandonment of the nest. Thus, there is no safe way to visually ensure the individuality of BTDs during the breeding season.

Table 4. The order of selected variables in classification of the male yodels into different territories based on stepwise discriminant analysis. Variables DI2, FIBE and FR12B were removed ($p > 0.05$).

Number in	Variables	Partial r^2	F	P-value
1	FR12E	0.98	743.4	<0.0001
2	DR1	0.92	179.4	<0.0001
3	DI	0.87	99.7	<0.0001
4	FI2E	0.86	94.1	<0.0001
5	FR1BE	0.70	35.3	<0.0001
6	DR11	0.69	34.1	<0.0001
7	DGAP	0.69	33.5	<0.0001
8	DI1	0.67	30.1	<0.0001
9	FI1	0.63	25.9	<0.0001
10	FR11	0.53	17.1	<0.0001
11	FR12C	0.32	7.1	<0.0001
12	FI2B	0.30	6.4	<0.0001
13	FR11C	0.18	3.3	<0.0001
14	FR12CA	0.10	1.6	0.0500

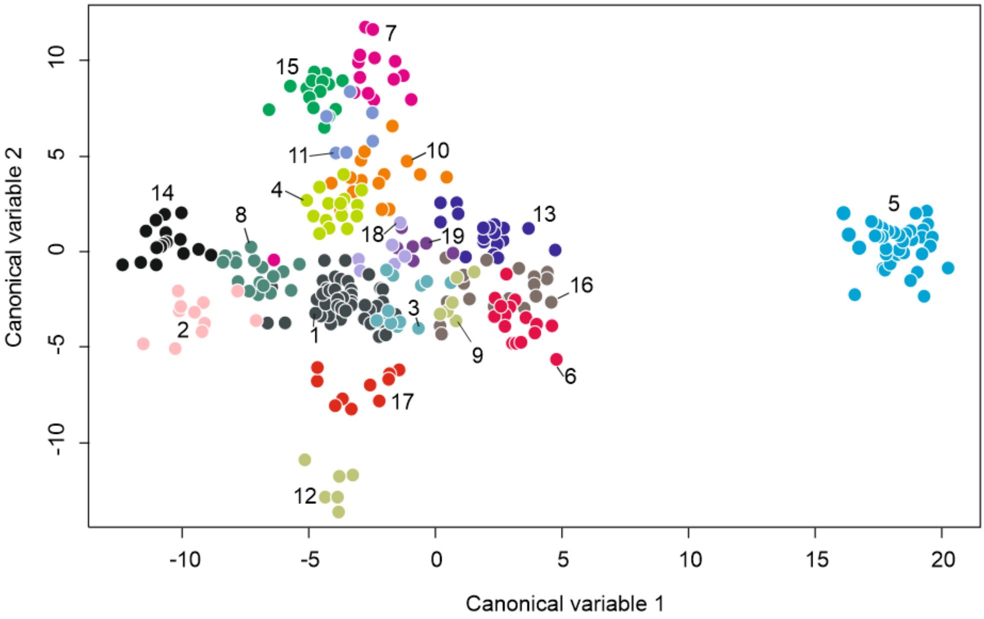

Fig. 5. The two canonical variables of all yodel data. The yodels in each territory are marked with different colours and the number refers to each territory. The yodel of BTDs in territory number 5 is clearly different compared to other yodels and territories (recording is available in the online supplementary materials). Color figure is available in the online version of this article.

Based on our results, the BTDs vocalization in specific territories remain the same from year to year. Thus, yodel characteristics are either territory-specific or individual-specific. The previous sounds unrealistic, and studies with the Common Loons show that the vocalization in specific territories remain the same from year to year. We have shown that the same BTD pair occupied the same territory during nine consecutive years (Lehtonen & Lappalainen 2017). On these findings, we assume that the yodeling is individual-specific and can be used to identify different males. At some point the males will be replaced and this yodel approach could be used to test if the yodel deviates from the previous.

The discriminant analyses showed that the individual males of Black-throated Divers can be differentiated from each other by their yodel in different territories. The overall misclassification rate was 2.02% based on cross-validation in all data. The highest misclassification rate, 10.46%, was observed in test data that included those territories that had two or more years of yodel data, and where only the last year of data was tested. The difference between these two analyses and misclassification rates (2.02 and 10.46%) is that on cross-validation only one song is classified at the same time against all other songs, while in the manual division all 96 songs are tested at the same time. The latter mimic situation, where the yodels were recorded in several territories over one summer and were then all classified based on earlier recorded yodels and thereby obtained discriminant functions.

The recent research on different bird species have shown that the spectral and acoustics variables of songs can be used to identify individual birds. Favaro *et al.* (2015) measured 31 spectral and temporal acoustic variables of the calls of the African penguin (*Spheniscus* sp.). The acoustic variables were used in a stepwise discriminant analysis, which classified correctly 66.1% of the contact calls and 62.5% of display songs to the correct individual bird. Similarly, Chang *et al.* (2018) showed that discriminant analysis classified correctly 94.5% of the individuals of Large-tailed Nightjar (*Caprimulgus macrurus*) based on nine vocal variables. In another nightjar species, *Caprimulgus europaeus*, Raymond *et al.* (2020) found that the male songs were correctly classified at a maximum of 73.5% within one season, rising to 75% if full-length calls and 13 acoustic variables were used. Yee *et al.* (2016) showed that the individual territorial calls of Sunda Scops-owls (*Otus lempiji*) can be correctly classified with 97.1% accuracy with discriminant function analysis.

In the BTD male yodel, duration and frequencies of the different parts of the introductory phrase and the first repeat phrase (Table 1) were found to be the most important in the identification. The repeat phrases, usually 2–4, are very similar to each other. When experimenting with the data, the variables also from the second repeat phrase were included in the analyses, but it was found that these have no added value in the individual identification of BTDs and therefore these were excluded from further analyses.

The success of the recording is affected by the size of the territory and the choice of the recording location. The size of the territory of the BTD pair varies from ten to one hundred hectares, depending on the environment and the nesting phase (Lehtonen 1970). Recording is only possible in calm and rainless weather, otherwise the sound of waves and rain will interfere. The maze of territory with its small islands can weaken the quality of recorded yodels. Often the territory is the whole island, and when a BTD circumnavigates its territory, the yodel may come from behind the island, making it unusable.

The duration from the beginning of the yodel to the end of first repeat phrase varies considerably in different territories. It was difficult for the human ear to distinguish the voices of most other BTDs, but it was possible to perceive the pace of the introductory phrase and the first repeat phrase as slow or fast. Another example of yodel that can be distinguished by human ear is the yodel of the territory 5. This is due to sudden change in frequency during the second note of the introductory phrase and the second note of the first repeat phrase: The sudden change rises the frequency about 350 Hz.The male of the territory 11 also raises his song during the second note of the introductory phrase.

Walcott *et al.* (2006) observed that male Common Loons changed their yodels either the first or second year on the new territory when they changed their 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. Such a change was not observed in the present study, and therefore the results suggest that no territory changes occurred during the study period.

The results here based on male yodels suggested that the same male BTDs occupy the same territory from year to year. Similar results were found for both male and female BTDs based on their breeding plumage in an earlier study in the same area (Lehtonen & Lappalainen 2017). Thus, these two studies are mutually supportive. However, individual identification by the vocal repertoire of males gives lower misclassification rates than using the breeding plumage based on discriminant analyses. Further, recording the yodels are much easier to carry out and causes minimal disturbance to BTDs than using the breeding plumage. However, the use of breeding plumage is valuable if data are also needed from females.

The main reason for using vocalization for individual identification is that the technique causes minimal interference, making it particularly suitable for BTDs that are sensitive to interference. The vocalizations in specific territories remain the same which probably suggests that these are the same individuals from year to year. Future studies should assess if yodels can be used to identify individuals by comparing yodel with other individual characteristics such as plumage or the use of ringed individuals.

Yksilöllinen vaihtelu kuikkien (*Gavia arctica*) reviirihuudoissa

Kuikkien (*Gavia arctica*) kuuluva reviirihuuto on tunnetuimpia luonnonääniä pohjoisilla alueilla. Tutkimuksen tavoitteena oli selvittää, voidaanko koiraskuikkia tunnistaa yksilöllisesti huudon perusteella. Vuosina 2018–2021 äänitettiin 19 urospuolisen kuikan reviirihuuto, 10 niistä 2–4 peräkkäisenä vuotena ja yhdeksän yhtenä vuotena. Äänitykset tehtiin samalla järvialueella Suomessa. Huuto koostuu yhdestä johdanto-osasta ja yhdestä tai useammasta toisto-osasta. Johdanto-osan ja ensimmäisen toisto-osan spektrogrammeista mitattiin 17 eri parametriä. Nämä koostuivat spektrogrammin eri osien taajuuksista ja kestoista. Valitut parametrit analysoitiin tilastollisesti. Erotteluanalyysiä käytettiin tutkittaessa kuikkayksilöiden yksilöllistä tunnistamista reviirihuutojen (n = 297) spektrianalyysin perusteella eri reviireillä (n = 19). Analyysit osoittivat, että käytettäessä 14 muuttujaa ja ristiinvalidointia, pystyttiin reviirit luokittelemaan huudon perusteella lähes 98 prosenttisesti oikein. Tämä viittaa siihen, että samat yksilöt puolustavat reviiriään vuodesta toiseen.

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Online supplementary material

The supplementary material contains information about the average duration (Fig. S1) and the average frequencies (Fig. S2) of yodels in different territories. Possible abrupt changes in frequency of the second note of the introductory phrase and repeat phrases are shown in Fig. S3. Misclassified yodels in the discriminant analysis after cross-validation are presented in Tables S1 and S2. The song/voice recording includes the exceptional yodel of the BTD male in territory 5 compared with the more typical yodel of the territory 1.