INDIVIDUALITY IN SCOPS OWL *OTUS SCOPS* VOCALISATIONS

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ABSTRACT

The focus of this study was to determine whether individual vocal identification of Scops Owls *Otus scops* was possible and if there was a stability of the hoot-calls over a short time period in the same individuals. Spontaneous vocalizations of 13 owls were recorded in 2004 in Southern Tuscany, Italy. Visual analysis of spectrograms and quantitative multivariate analysis of six vocal features showed marked individual differences. In some owls a repertoire of two different hoot types was found. In 2005, 10 Scops owls were recorded three times in the same breeding season (2 hours and 10 days after the first session). Statistical analysis of data showed that 60% of owls did not change call features over time. However a slight but significant variability between successive vocal performances of the same owl was found in 40% of cases. This variability may decrease the recognition power by acoustic analysis. To overcome this obstacle I suggest a multi step qualitative/quantitative approach. A Difference Index (DI) was calculated to set a threshold between the slight intra-individual and the very high inter-individual variability. This method allowed the recognition of calls of each owl recorded over time in 2005.

Keywords: Scops Owl, Otus, vocal identification, vocal individuality, vocal variability

INTRODUCTION

Many studies have shown the presence of individual vocal features in a wide range of animal species. Terry *et al.* (2005) suggest that vocal individuality is most likely a feature of all vocally active species, caused by a series of genetic, developmental and environmental factors. There is a general agreement between research workers that individuality exists and can be shown using qualitative/quantitative spectrographic analysis (Catchpole & Slater 1995). Vocal individuality has been demonstrated in oscine (Lind *et al.* 1996; Christie *et al.* 2004; Gentner & Hulse 1998; Aubin *et al.* 2004; Weary *et al.* 1990;

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McGregor *et al.* 1994), suboscine (Lovell & Ross Lein 2004; Bard *et al.* 2002; Haven Wiley 2005) and nonpasserine birds (Mathevon *et al.* 2003; Galeotti & Sacchi 2001; Galeotti & Pavan 1991; Delport *et al.* 2002; Tripp 2004; Peake *et al.* 1998; Lessells *et al.* 1995; Gilbert *et al.* 1994; Lengagne *et al.* 2001; Jouventin & Aubin 2002). However it is still matter of debate which are the most important individual song signatures. A criterion to select the most useful individual acoustic signatures is a higher between-individual variation compared to a lower within-individual variation for a given feature (Terry *et al.* 2005; Christie *et al.* 2004). This has led to a very broad spectrum of different acoustic characteristics utilized in studies on different bird species: time and frequency parameters (Christie *et al.* 2004; Lessells *et al.* 1995); analysis of the song repertoire of a bird species (Weary *et al.* 1990); the complex time structure existing in different part of a call (Peake *et al.* 1998); the utterance rhythm of a call or a song syllable (Galeotti & Sacchi 2001; Searby *et al.* 2004).

Clearly, finding some vocal characteristics with high individual differences does not mean that these are used by the bird itself to recognize conspecifics. How birds discriminate between different conspecifics is an even more complex research topic and to date there are only a few relevant studies. European Starlings *Sturnus vulgaris* seem to rely – at least in part – on memorization of individually specific song types (Gentner & Hulse 1998) and Gentner (2004) has shown the underlying neural mechanism of this ability. Other studies outlined the importance of song repertoires in oscine birds (Riebel & Slater 2003; McGregor & Krebs 1982; Krebs 1976; Slater 1983). Nelson (1989) found that frequency variation of Field Sparrow song *Spizella pusilla* affected individual recognition. Penguins of the genus *Apdenodytes* use a double coding system that integrates information in both the temporal and frequency domain, while penguins of the genus *Pygoscelis* use a simpler parameter: the pitch of the call (Lengagne *et al.* 2001; Jouventin & Aubin 2002; Aubin *et al.* 2000). The studies cited above suggest different mechanisms in different bird species and analyze a broad spectrum of vocal parameters to discriminate between individuals. Therefore a deep knowledge of the vocal activity and song structure of a given bird species is a prerequisite to achieve the best results in this research topic.

Individual vocal signatures could provide a very useful non-invasive marking method for recognizing individuals and/or as a census tool. Endangered and cryptic bird species that are difficult to catch and are prone to harm during capture and handling could benefit particularly from a non-invasive marking method. As well as monitoring population trends, identifying individuals can highlight behavioural traits that may have a conservation value: for example the reproductive success of a different subsection of a population

and the site fidelity during successive breeding seasons for migrant birds. Another important implication is a better knowledge of the communication behaviour in animals, which can benefit from a deeper knowledge of the mechanisms of individual recognition in birds.

The aims of this work are: i) to define the characteristics of Scops Owl calls, ii) to investigate whether a difference exists between individual vocal activity and if so, to find what acoustic parameters are involved, iii) to show whether there is vocal stability over a short time period within the same individuals. The Scops Owl is a migrant nocturnal raptor, which has a highly territorial behaviour during the breeding season. In Tuscany it is a regular migrant species, which in October flies to Africa, except for a few sporadic cases of wintering. Estimated density in the study area is 9-11 territories/100 km^2 (Dragonetti unpub. data), which is comparable to 3-20 territories/100 km^2 found in Northern Italy (Sacchi et al 1999) and to about 2–7 territories/100 km^2 found in Tuscany (Brichetti & Fracasso 2003). The breeding territories are defended with a very intensive vocal activity: a whistling "kiu" repeated over and over with clockwork regularity (hereafter also referred as "hoot"). Galeotti & Sacchi (2001) showed a significant difference between calls of different male owls in response to playback stimulus: a re-identification of the individuals was made after one year. In the present study I analyzed the spontaneous vocal activity without playback stimulus, as it could alter the motivational status of the bird, which in turn could strongly influence vocal output and vocal features (Eakle *et al.* 1989; Appleby & Redpath 1997). Moreover, playback can also having biasing effects, for example by causing individuals to move off their territories (Terry *et al.* 2005). The individual re-identification technique by mean of voice analysis requires vocal stability over time, which is difficult to show because ideally it needs independent identification of recognizable individuals. As the studies involving owls (Galeotti & Sacchi 2001; Delport *et al.* 2002) – the present one included – did not use individually recognizable birds, the temporal stability of calls is assumed true when vocal parameters are stable for the bird singing in the same territorial boundary. Although it is reasonable, this assumption is risky when referred to a long time period (e.g.: one or more years), because we do not know if all vocal parameters remain constant or if there is a modification also for the same bird. Long term studies on radio-tagged Bitterns *Botaurus stellaris* found contrasting results for vocal stability over time: Puglisi & Adamo (2004) found that vocalization of the same males were not stable over time, while Gilbert *et al.* (2002) were able to re-identify booming males in Britain over a nine year period. Therefore, if some modification in vocal parameters takes place over a long time period in the same individual, the re-identification could fail leading to an error. To avoid this risk I tested vocal stability within individuals over a short time period; in this case the likelihood

of a territory owner change is minimized and the assumption that the same territory means the same bird can be considered true.

Recording and spectrographic analysis

Calls of Scops owls were recorded on analogue audio cassette recorder Marantz PMD 222 with an Audiotechnica AT815b shotgun microphone and were digitized with a standard A/D converter of a personal computer sound card. Sampling rate was 48 kHz with 16 bits accuracy. I analyzed the recordings using SeaWave v. 1.1 software (Gianni Pavan, Lab. of Bioacoustics, Pavia University, Italy), with the spectrogram parameters set as following: FFT size = 2048 points, scan step = 512 points, Window type Gaussian, overlap = 75%. SeaWave software generated spectrograms and the corresponding oscillograms (frequency resolution = 23 Hz and time resolution = 11 ms). I measured the vocal parameters with the cursor on the computer screen. Frequency measurements were done on the spectrogram, whereas time measurements were done on the oscillogram. SeaWave keeps also track of the dominant frequency (frequency associated with the highest amplitude), plotting it on the spectrogram (not shown in figures).

All recordings were made from a distance varying from 15 to 40 m. and between 9.30 pm and 1.00 am, the period when calling was commonest. Each owl territory was checked several times to perform a recording of a sufficient long bout of spontaneous vocal activity. In the present study, spontaneous vocal activity means that it was not induced by playback of conspecific calls.

It is well known that female Scops owls sometimes call at the beginning of breeding season, while during late summer (the period when the present study was performed) they seldom call, performing antiphonal duets with their mates (Galeotti *et al.* 1997; Cramp 1985). I did not use recordings from such duets, therefore all calls reported in this paper should belong to males.

Scops owl vocal features and individual differences

To investigate individual differences between owls a study was carried out in the southern part of Grosseto district, a hilly area between 11°00'/11°25' Long. E. and 42°10'/42°45' Lat. N. Recordings of 13 owls were made in 2004 during the breeding season from June 1 to July 30 in 13 different territories, which were on average 3.9 km apart from each other. The distances between two territories

ranged from 0.5 to 8.5 km. However only in two cases (owl 17 vs 18 and owl 28 vs 29) the distances were less than 1 km; in these cases the simultaneous hooting allowed me to be sure that there were four different individuals. In all other cases the distances of the territories ranged from 3.5 to 8.5 km, well above the mean width of a Scops Owl territory (Cramp 1985). Moreover the recordings in the neighbouring territories were all performed in the same night, so it is almost impossible that the same owl has been recorded in different territories. In conclusion I am confident that these 13 recordings belong to different individuals. A total of 39 minutes of recording was made for all these owls, with a minimum of 23 hoots recorded per owl. The following temporal and frequency parameters were measured (see Figure 1): Freq A = maximum frequency (frequency of point A in Figure 1); Freq B = dominant frequency at the beginning of hoot (point B); Freq C = dominant frequency at the end of hoot (point C); Avg BC = average dominant frequency between point B and C; FM BC = frequency modulation between point B and C expressed as sum of increases and decreases in absolute value between point B and C; Rhythm (R) = time interval between two consecutive hoots; Dur
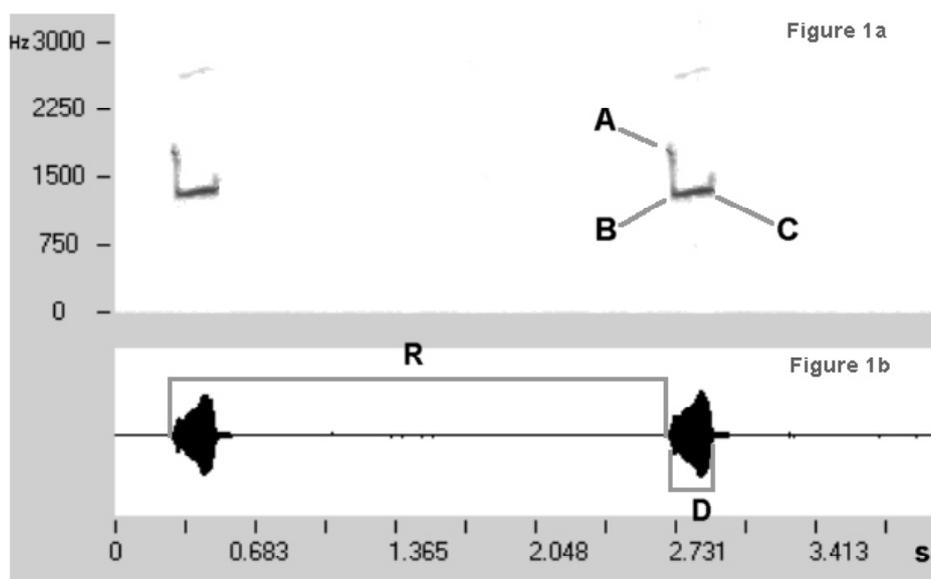

Figure 1. Features of Scops owl calls. Spectrogram (Figure 1a) and oscillogram (Figure 1b) of Scops owl hoots with parameters measured for individual recognition. Freq A = maximum frequency; Freq B = dominant frequency at the beginning of hoot; Freq C = dominant frequency at the end of hoot; Avg BC = average dominant frequency between point B and C; FM BC = frequency modulation between point B and C expressed as sum of increases and decreases in absolute value; Rhythm (R) = time interval between two consecutive hoots; Dur (D) = duration of hoot.

(D) = duration of hoot. As shown in Figure 1 it is evident that the dominant frequency coincides with the fundamental one. The temporal parameters are expressed in milliseconds (ms) and frequency values are in Hertz (Hz).

Preliminary experiment

Since I have recorded only the *spontaneous* calls of Scops owls, it was impossible to standardize the distance in the different recording sessions and in some cases there were obstacles (mainly foliage, trees or hedgerows) between microphone and bird. To avoid the use of vocal parameters affected by these variables, I tested the effect of distance and foliage on the recorded hoots. This was achieved by a preliminary experiment, in which 20 good quality Scops owl hoots were broadcasted at increasing distances of 15-40-80 meters. These hoots were then recorded with the same apparatus described above. The broadcasting was done in 2 different conditions: without foliage and with foliage between the microphone and the loudspeakers, which were placed at about 7 m. above the ground. The foliage obstacle was a natural hedgerow with trees and bushes (10 m. tall) 10 m. from the broadcasting source. The same 20 hoots were played successively for the three chosen distances in a flat field without obstacles. For the second condition (foliage obstacle), the sound source was displaced behind the natural hedgerow which bordered the same field. The same hoots were then played and recorded successively at the specified distances. The broadcasting chain was composed of a portable PC with a standard analogue audio output directly connected to two 15 W Sharp amplified loudspeakers. The broadcast file was a 48 kHz digitized recording of Scops owl calls; the sound pressure level was set at 85 dB at 1 m distance from source. I evaluated the effect on the maximum frequency and average dominant frequency (Freq A and Avg BC, see Figure 1). The effect on harmonic content was also checked, where harmonic content of a given hoot was expressed as the ratio between the amplitude of the first harmonic frequency and the relative amplitude value of the correspondent fundamental frequency. Each vocal parameter was submitted to Friedman ANOVA.

Vocal stability within individuals over a short time period

To assess vocal stability a further study was carried out in 2005 in the same area as described above. I recorded 10 owls in 10 different territories from June 25th to July 30th. During this period spontaneous singing activity in the study area was consistent and fairly stable; spontaneous vocal activity during summer was found

also for Northern Italy by Sacchi *et al.* (1999). Each individual was recorded three times: the second recording session was made 1-3 hours (mean 2) after a first baseline recording, the third recording session was held 6/11 days after the first one (mean 10.1). Each owl was recorded when singing from the same perch, except in two cases where the perches were at a distance of 20/25 m. from the place of the previous recording session. This scheme was adopted to be sure that the recorded owls were the same individuals during all three successive recordings. I recorded a minimum of 3 minutes of continuous singing activity for each session for each owl; the total recording time for this study was 105 minutes. I could find nine out of ten owls present in their respective territories during all the duration of the study, while one (owl 32 – see Figure 6) abandoned the territory after the first day of recording. This territory was not reoccupied by another Scops owl during that breeding season. The same parameters as in the 2004 study were measured, except for FM BC which was found to have a low discriminant power between individuals (see results below) and for this reason was not included in the 2005 study.

Analytical methods

The reliability of qualitative visual analysis of spectrograms and its effectiveness for discriminating between different individuals was tested in a preliminary experiment: 9 randomly selected spectrograms of two subsequent hoots for each of the 13 owls (2004 study) were submitted to 3 "naive" observers, which were unaware of the experimental design. The observers were asked to classify the spectrograms using Figure 2 as a reference. The significance of the number of correct matches was checked by means of binomial test (Siegel 1956) under H_0 = distribution by chance (that is calculated as random probability of 1/13 of assigning a sonogram to the correct male).

All the quantitative measures described above were submitted to Shapiro-Wilk test and Liliefors test to check for normality. Both tests indicate that the data were not normally distributed (Shapiro-Wilk test p < 0.001). Moreover a comparison of the variances of most samples showed a lack of homogeneity. Therefore I used nonparametric statistical methods to test the significance of differences between and within owls.

I submitted hoot parameters measured from different birds to Kruskall-Wallis test to check for individual variation in each parameter and I used Mann Whitney-U test to perform pairwise comparisons. To assess the overall difference between individual scops owl calls I performed a Non Parametric Multivariate Analysis
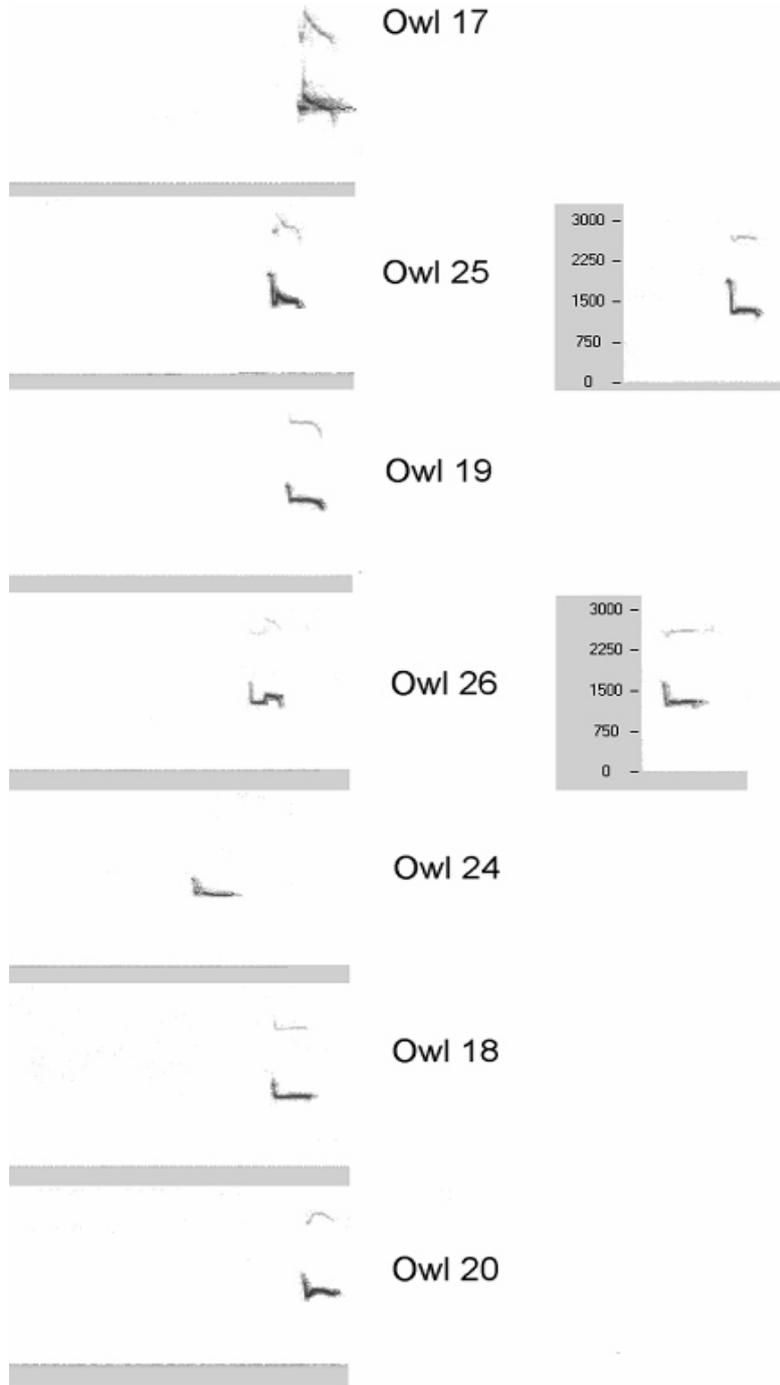
Figure 2. Spectrograms of Scops Owl recorded in 2004. On the right there are examples of strongly modified hoots (owl 25, 26)
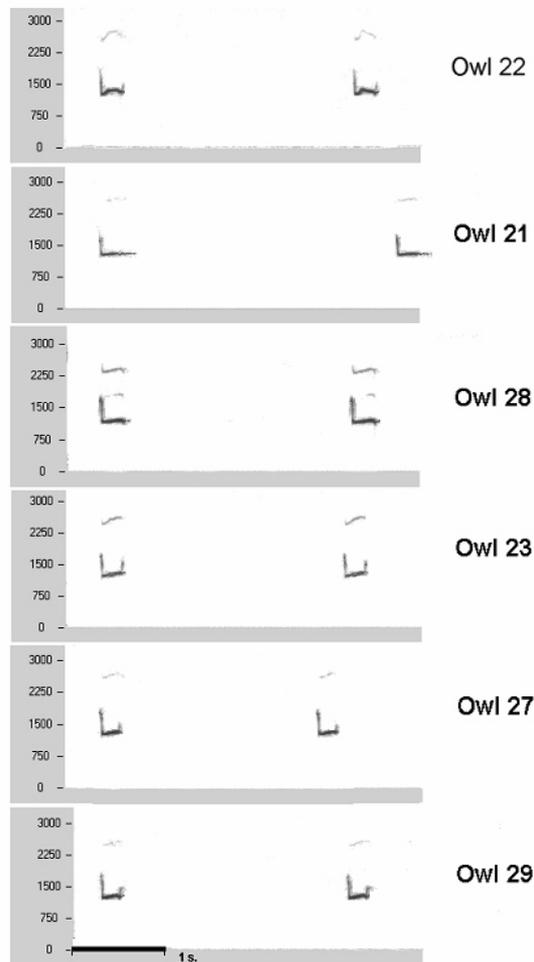
Figure 2 (continued)

of Variance (NPMANOVA; Anderson 2001) using correlation distance measure. Vocal stability within owls was tested for each vocal parameter by means of Friedman ANOVA. If Friedman test was statistically significant, I performed univariate Wilcoxon rank test and multivariate paired Hotelling T2 test to check for differences between different recording times. The results of statistical tests were considered significant when the Null hypothesis (H_0) had a probability lower than 0.01.

For the 2004 study I calculated the between-owl Coefficient of Variation for each vocal parameter (CV_b) and the average within-owl coefficients of variations (CV_w) based on the values from calls of each owl. The CV was calculated following the formula: CV = $100*(1+1/4n)*sd/m$ (Aubin *et al.* 2004; Scherrer 1984), where n =

number of observations, sd = standard deviation, m = mean. The ratio of between-owl to within-owl coefficient of variation (CV_b /CV_w) was used as a measure of the identification power of each vocal parameter: a higher value suggests a vocal feature is more variable between individuals relative to its variability within individuals and could be used as a cue to individual identity (Christie *et al.* 2004). A parametric Multivariate Analysis of Variance (MANOVA) was also performed and Canonical Variate Analysis (CVA) was used as a descriptive tool to evaluate how well linear combinations of the selected acoustic features could separate calls according to the identity of the singer. CVA produces a scatter plot of specimens along the two first canonical axes, producing maximal and second to maximal separation between all groups (multigroup discriminant analysis). The axes are linear combinations of the original variables as in Principal Component Analysis (Hammer *et al.* 2004). The eigenvectors of each variable is a measure of variable "loading" on each axis (Campbell & Atchley 1981) and was used (as an alternative method to CV_b /CV_w ratio) to calculate the relative identification power of each acoustic parameter between different owl calls.

In total I analyzed 831 hoots. For most owls I randomly selected 20 hoots from each recording session; only for 3 owls there were less than 20 hoots available for analysis. In these cases (1 is relative to a "secondary" call type – see results below) all available hoots were used and the total number of data is declared in the footer of the table. When the number of data points is not declared, it is implied that it is equal to 20 for each group.

A cross validation test was performed to check the reliability of classification. I randomly split the data set of each recording session of each Scops owl into two halves. Pairs of data subsets were randomly selected and then submitted to a multivariate Paired Hotelling T test. Testing data subsets from same or different owls should give statistically different results and therefore should allow a correct classification of owls. This was done for 46 randomly selected comparisons between and within owls.

Statistical analysis was done using PAST (Hammer *et al.* 2004) and Stats4U software packages.

RESULTS

Features of Scops Owl hoots

The hoot of Scops owl consists of a single syllable lasting 180-350 ms, monotonously repeated every 2300-3200 ms. The average fundamental frequency ranges from 1150 to 1450 Hz, while maximum frequency reaches 1600-1900 Hz. Figure 2 shows the spectrograms of

two consecutive hoots of all 13 Scops owls recorded in 2004. Visual analysis of spectrograms showed that in 84.6% of owls recorded in 2004 the hoots were fairly stable, with only minor variations. A strong variation of the spectrogram was found in 15.4% of owls (see Figure 2 – owl 25 and 26) in 8.4% and 22.2% of all hoots (mean 16.4%). These strongly varied calls suggested a switching to a different call type. These findings were confirmed by the visual analysis of calls recorded in 2005: 60% of owls showed no or very slight variation, while 40% of owls showed strong variation in average 16.3% of all hoots (16% for owl 35, 17.3% for owl 43, 17.6% for owl 49, 8.7% for owl 60). Note that in 2005 study each owl was recorded for a minimum time of 9 minutes in 3 different sessions, while in 2004 I recorded only one time each owl with a minimum of 1.5 minutes. This increase in recording time could explain the relatively higher presence of a second call type found in 2005 study.

To define a second call type I used the following criterion: a vocal performance must have at least five consecutive hoots or at least 5% of all hoots showing a marked difference in spectrograms. Figure 7 and 8 show the second call type for all Scops owls recorded in 2005. None of the owls studied showed more than 2 different call types.

In those owls which showed 2 different call types, each vocal performance was characterized by a preferred call type that was sung for more than 70% of hoots. In 20% of owls recorded in 2005 the second call type appeared only in the second or third recording session, while it was absent in the previous ones. Moreover 20% of owls (in 2005 study) showed a different preferred call in the second or third recording session: the secondary call type of the previous recording became the preferred call in the following session. In my quantitative analysis of call stability over time of owls with two different call types, I have compared the two different call types separately.

Some of the spectrograms in Figure 2 and Figure 6 show also the presence of a first harmonic frequency of variable amplitude. This spectrographic evidence is reported also by Cramp (1985). Therefore I have taken into account this feature when performing visual analysis of spectrograms and I have measured its relative amplitude, as described in the methods section.

Reliability of visual analysis

Figure 3 shows the percent of correct matches obtained with visual qualitative analysis of randomly selected spectrograms from the calls recorded in 2004. A correct identification between different individuals was obtained in 94.4% of cases over a total of 117 tests. The hoots of ten owls were correctly attributed in 100% of cases, while for

three owls (owl 24, 27, 29) the percentages of correct matches were respectively 88.9, 66.7 and 77.7. All these data are statistically significant if compared with a matching by chance (p < 0.001 Binomial test). Clearly the three owls which have the most similar hoots are 29 vs 27 and 27 vs 23, because all the incorrect matches of owl 27 were done with hoots of owl 23 and the incorrect matches of owl 29 were done with hoots of owl 27.

Preliminary experiment: effect of distance and foliage

Freq A, Avg BC and harmonic content did not change between hoots recorded without obstacles at 20–40–80 meters from the broadcasting source. Friedman test between all three distances for the three parameters considered was not significant ($\chi R^2 < 2.3$ for all tests). The presence of foliage between audio source and recording microphone did not significantly affect Freq A and Avg BC at all distances ($\chi R^2 < 4$ for all tests), while it strongly reduced the harmonic content of hoots both at 20 and 40 meters from source ($\chi R^2 > 14$, p < 0.001). Interestingly the harmonic content of hoots recorded at 20 meters was more strongly reduced than that of hoots recorded at 40 meters ($\chi R^2 = 11$, p < 0.001), suggesting that the closer the foliage was to the microphone, the higher was this reduction. In conclusion, foliage combined with distance significantly affected the amplitude of the first
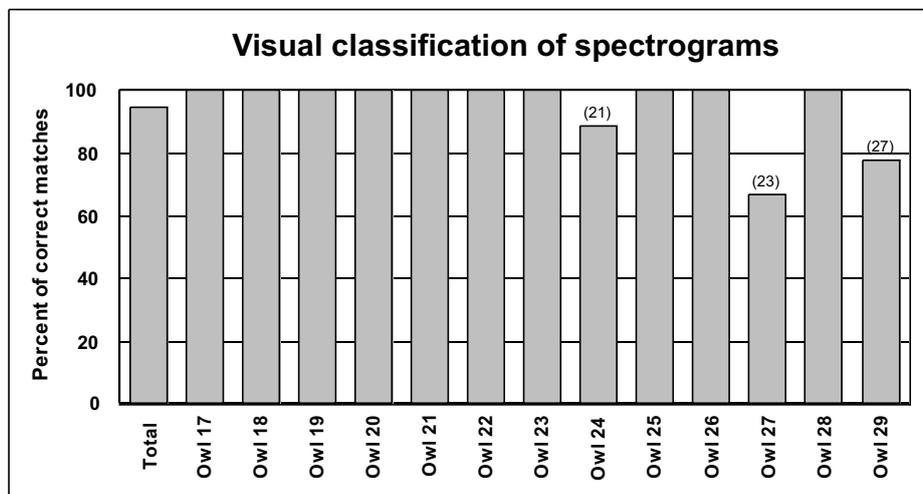

Figure 3. Reliability of visual classification of hoot spectrograms by "naive" observers. Nine hoots were randomly selected for each owl and submitted to the observers. First column is % correct matches for all tests (n=117). Other columns are % of correct matches for each owl. Numbers above the columns show the mismatched test results

harmonic, while the fundamental frequencies did not change. For this reason I have not included the harmonic content in the subsequent quantitative analysis.

Individual differences between owls

Table 1 shows all the data for Scops owls recorded in 2004 study. Univariate analysis for each frequency and time parameter by means of Kruskall-Wallis test yields highly significant differences (Hc > 190 for all tests; p < 0.001). Multivariate NPMANOVA yields the same result between owls (F > 2000; p < 0.0001).

Although the correct statistical approach for these data is a non parametric test (see Methods above), I have performed also a parametric Multivariate Analysis of Variance (MANOVA) and a Canonical Variate Analysis (CVA): the results of MANOVA are highly significant too (F = 284; p<0.001). CVA scatter plot (Figure 4) clearly indicates that linear combinations of the selected acoustic parameters yields a very good separation between different individuals. CVA also shows that owl 23 and owl 29 have the most similar call types. This confirms, at least in part, the results shown in Figure 3. The values of eigenvectors for each acoustic parameter (Figure 5) indicates that Rhythm, Avg BC and Freq B are very important for discriminating

TABLE 1

Frequency and time measurements for all owls (2004). Means and standard deviations (in brackets) of all vocal parameters of Scops Owl calls recorded during breeding season 2004. Frequency parameters are expressed in Hz, while time measurements are in ms. *Freq A* = maximum frequency; *Freq B* = dominant frequency at the beginning of hoot; *Freq C* = dominant frequency at the end of hoot; Avg BC = average dominant frequency; *FM BC* = increases and decreases of dominant frequency (frequency modulation); *Rhythm* = time interval between the beginning of hoots; *Dur* = hoot duration.

|	Freq. A	Freq. B	Freq. C	Avg. BC	F.M. BC	Rhythm	Dur.
Owl 17	1913 (19)	1247 (16)	1355 (22)	1417 (13)	449 (83)	3203 (9)	263 (12)
Owl 18	1663 (29)	1272 (11)	1279 (14)	1279 (8)	44 (20)	3050 (60)	301 (14)
Owl 19	1771 (13)	1419 (18)	1282 (20)	1354 (18)	144 (17)	3121 (26)	278 (12)
Owl 20	1752 (28)	1328 (11)	1368 (22)	1364 (12)	165 (35)	3224 (13)	250 (9)
Owl 21	1750 (23)	1285 (9)	1292 (8)	1296 (7)	32 (16)	3320 (21)	258 (17)
Owl 22	1881 (17)	1305 (11)	1342 (15)	1342 (9)	155 (37)	2804 (26)	247 (9)
Owl 23	1773 (13)	1234 (12)	1314 (7)	1279 (11)	106 (49)	2703 (7)	248 (6)
Owl 24	1670 (18)	1392 (18)	1343 (12)	1364 (9)	62 (16)	2375 (16)	301 (16)
Owl 25	1900 (13)	1332 (8)	1283 (26)	1352 (13)	263 (52)	2987 (18)	231 (10)
Owl 26	1663 (13)	1270 (10)	1291 (78)	1315 (23)	277 (55)	2815 (13)	267 (21)
Owl 27	1898 (13)	1318 (10)	1361 (21)	1342 (16)	56 (37)	2443 (35)	219 (8)
Owl 28	1794 (20)	1175 (12)	1187 (14)	1182 (7)	53 (21)	2771 (11)	289 (8)
Owl 29	1798 (33)	1245 (8)	1270 (14)	1265 (7)	70 (21)	2719 (13)	219 (7)

Scatter plot of Canonical Variate Analysis
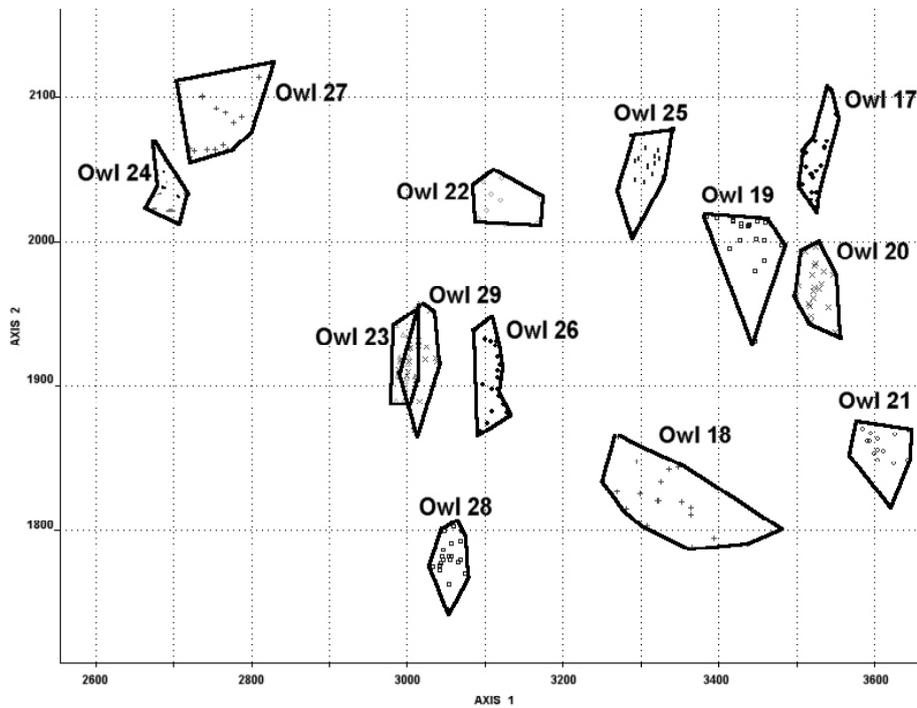
Figure 4. X axis and Y axis represents the two most important components found by CVA. These components are linear combinations of all vocal parameters that optimally separate calls according to the identity of the singer.

between individuals. Freq A plays a role, but is less powerful for identification; FM BC, Dur and Freq C are less important. To assess the relative importance of each vocal variable I have also studied the coefficients of variations (CV): the results shown in Table 2 confirm those obtained with CVA. Rhythm, Freq B and Avg BC are the most individually distinctive measures. Freq A has a lower but not negligible discriminating power, while Dur, Freq C and FM BC are less important. The within-owl variability is very low for Rhythm ($CV_w = 0.7$) and very high for FM BC ($CV_w = 32.6$): the reliability of FM BC measure is quite low. Therefore I decided to exclude FM BC parameter from the 2005 study, because it shows a poor reliability and a low discriminant power between individuals. I have performed some pairwise comparisons between the "most similar" owl calls (23, 27, 24, 19, 20 and 29 following visual analysis of spectrograms and CVA scatter plot). In all cases NPMANOVA and Paired Hotelling T2 test show a highly significant difference between these most similar owls (p<0.001). While most comparisons yield very high (>1000) F

TABLE 2
Within-owl and between-owl coefficient of variability (CV) for seven song features.
Ratio is CVb/CVw.

	Freq A	Freq B	Freq C	Avg BC	F.M.BC	Rhythm	Dur
Within	1.106	0.924	1.631	0.889	32.57	0.727	4.433
Between	5.235	4.982	4.203	4.447	85.53	9.847	11.285
Ratio	4.733	5.392	2.577	5.002	2.626	13.544	2.546

values, one case (29 vs 23) yields a relatively lower F value (F = 14). In this last case I compared each vocal feature using U-Mann Whitney test: all but FM BC were significantly different (p < 0.01). Paired comparisons of all vocal features for owls 27, 24, 19 and 20 yielded always significant differences. In conclusion, the most similar calls show a consistent significant difference between individuals for almost all time and frequency features.

The results of cross validation test (see methods – Analytical methods) were clear-cut: all comparisons within the same owls yielded not significant values (HotellingT2 always less than 50 and in most cases between 5 and 15), while all comparisons between owls yielded highly significant values (HotellingT2 always above 203 and in most cases above 1000; p < 0.01).

Vocal stability within individuals over a short time period

Spectrograms of the same owl recorded 2 hours and 10 days after the first baseline recording show a remarkable constant structure (Figure 6). Owl 35 and owl 49 sing two different call types and they change their preferred call type in different vocal performances. Figures 7 and 8 show the second call type for owls 35, 49, 43 and 60. Owl 35 and 49 sing a second call type in two different recording sessions: visual analysis of spectrograms shows that also this second call type does not change over time. Owls 43 and 60 show a different call type only in one recording session (see Figure 8).

Quantitative analysis of spectrograms shows that the *between* owls difference, found comparing baseline recordings of all different owls of 2005 study, is striking (NPMANOVA: F = 2115; p < 0.0001) and confirms the results of 2004 study. Table 3 shows a *within* owl call stability over time in 6 out of 10 cases: Friedman ANOVA yields not significant values for all vocal parameters. One of these 6 stable owls show a significant difference (p < 0.01) only for the second call type (see owl 35b – Table 3), due mainly to a slight shift in Rhythm, while the first call type of this same owl is nicely stable (see Table 3, owl 35). Yet the calls of 4 owls vary slightly over time: the Friedman

TABLE 3

Vocal stability over time within owls. Means and standard deviations (in brackets) of all vocal parameters of Scops Owl calls recorded during breeding season 2005. Each owl was recorded three times: first baseline recording, 2 hours after baseline, 10 days after baseline. Frequency parameters are in Hz, while time measurements are in ms. Freq A = maximum frequency; Freq B = dominant frequency at the beginning of hoot ; Freq C = dominant frequency at the end of hoot; Avg BC = average dominant frequency; Rhythm = time interval between the beginning of hoots; Dur = hoot duration. 35b and 49b are the second song types of Owls 35 and 49.

		Freq A	Freq B	Freq C	Avg BC	Rhthym	Dur
Owl 31							
Friedman ANOVA chi-r-square	First rec.	1768 (25)	1299 (12)	1326 (33)	1313 (20)	2512 (16)	248 (27)
<5 (n.s.) for all parameters	2 h	1764 (41)	1302 (16)	1316 (15)	1316 (11)	2496 (18)	247 (19)
	10 days	1788 (24)	1292 (11)	1314 (25)	1313 (16)	2501 (17)	242 (19)
Owl 35							
N. of data=10; Friedman ANOVA	First rec.	1831 (16)	1412 (18)	1355 (29)	1396 (23)	2504 (100)	267 (20)
chi-r-square <1.7 (n.s.) for all	2 h	1827 (18)	1417 (19)	1353 (19)	1399 (13)	2504 (26)	274 (18)
parameters	10 days	1826 (23)	1419 (19)	1352 (28)	1399 (23)	2512 (37)	264 (19)
Owl 38							
Friedman ANOVA chi-r-square	First rec.	1814 (34)	1268 (21)	1271 (24)	1272 (13)	2859 (26)	238 (22)
=15.1 (p<0.01) for Rhythm;	2 h	1817 (28)	1266 (14)	1277 (12)	1272 (8)	2846 (13)	239 (15)
chi-r-square <1.8 (n.s) for all	10 days	1796 (40)	1267 (14)	1278 (16)	1275 (9)	2820 (19)	239 (21)
other parameters							
Owl 47							
Friedman ANOVA chi-r-square	First rec.	1747 (25)	1225 (10)	1247 (12)	1238 (8)	2871 (17)	323 (21)
>12.2 (p<0.01) for Rhythm and A	2 h	1729 (22)	1229 (10)	1256 (13)	1243 (9)	2872 (49)	327 (17)
vgBC; chi-r-square <1.8 (n.s) for	10 days	1746 (21)	1223 (23)	1257 (24)	1255 (16)	2822 (32)	336 (19)
all other parameters							
Owl 43							
Friedman ANOVA chi-r-square	First rec.	1793 (22)	1278 (14)	1347 (51)	1366 (14)	3054 (17)	329 (15)
<3.2 (n.s.) for all parameters	2 h	1783 (23)	1263 (13)	1355 (60)	1371 (21)	3052 (19)	339 (21)
	10 days	1777 (19)	1271 (23)	1329 (31)	1361 (19)	3063 (26)	335 (21)

Owl 49	First rec.	1800 (36)	1266 (31)	1317 (38)	1334 (23)	2893 (38)	270 (26)
N. of data=15; Friedman ANOVA chi-r-square <1.5 (n.s.) for all parameters	2 h	1793 (38)	1269 (33)	1299 (41)	1331 (28)	2885 (43)	270 (35)
	10 days	1807 (36)	1289 (19)	1312 (29)	1331 (24)	2889 (42)	276 (40)
Owl 53	First rec.	1854 (28)	1297 (19)	1306 (23)	1307 (13)	2996 (27)	315 (32)
Friedman ANOVA chi-r-square >9.6 (p<0.01) for Freq A and Rhythm; chi-r-square <5 (n.s) for all other parameters	2 h	1870 (26)	1288 (19)	1288 (22)	1295 (8)	3017 (17)	301 (21)
	10 days	1888 (26)	1294 (16)	1285 (21)	1297 (9)	3024 (35)	312 (24)
Owl 56	First rec.	1613 (22)	1185 (14)	1224 (33)	1210 (19)	3019 (21)	244 (17)
Friedman ANOVA chi-r-square <7.1 (n.s.) for all parameters	2 h	1612 (21)	1185 (12)	1203 (13)	1193 (7)	3021 (17)	244 (18)
	10 days	1610 (19)	1183 (12)	1202 (13)	1195 (6)	3010 (18)	244 (14)
Owl 60	First rec.	1867 (21)	1310 (15)	1249 (15)	1293 (8)	3007 (16)	238 (20)
Friedman ANOVA chi-r-square =10.2 (p<0.01) for Avg BC; chi-r-square <6.5 (n.s) for all other parameters	2 h	1867 (18)	1300 (16)	1258 (15)	1294 (7)	3004 (16)	239 (11)
	10 days	1869 (24)	1293 (18)	1248 (23)	1283 (10)	3011 (22)	242 (11)
Owl 32	First rec.	1784 (34)	1282 (17)	1278 (12)	1284 (8)	2913 (26)	285 (28)
Friedman ANOVA chi-r-square <6.2 (n.s.) for all parameters	2 h	1773 (28)	1275 (12)	1277 (14)	1276 (5)	2908 (21)	265 (18)
	10 days	–	–	–	–	–	–
Owl 35b	First rec.	1818 (25)	1268 (19)	1334 (21)	1342 (13)	2537 (24)	265 (16)
N. of data =10; Friedman ANOVA chi-r-square = 7.8 (p<0.01) for Rhythm; chi-r-square <5 (n.s) for all other parameters	2 h	1815 (29)	1270 (28)	1351 (20)	1350 (23)	2490 (31)	267 (14)
	10 days	–	–	–	–	–	–
Owl 49b	First rec	–	–	1305 (17)	–	–	–
N. of data=8; Friedman ANOVA chi-r-square <3,6 (n.s.) for all parameters	2 h	1807 (9)	1265 (14)	1305 (17)	1297 (5)	2884 (17)	270 (10)
	10 days	1809 (22)	1268 (15)	1293 (16)	1301 (11)	2872 (19)	273 (13)

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test values are a bit over the significance threshold (p < 0.01) only for one parameter (owls 38, 60) and for two parameters (owls 47, 53). Owls 38 and 47 show a stable call at 2 hours, while 10 days recording differs significantly from both basal and 2 hours (paired HotellingT2 test p < 0.01). Owl 53 showed significant difference at 2 hours and 10 days versus basal recording (HotellingT2 p < 0.01), but the comparison 2 hours vs 10 days was not significantly different. Owl 60 showed a significant difference between 2 hours and 10 days (p < 0.01), but not between basal recording versus 2h and basal versus 10 days.

In conclusion, the results of visual analysis show a general stability of Scops owl call over a short time, but quantitative analysis suggests that sometimes there is a very slight but significant variability between different vocal performances of the same owl. This finding suggests the need of a method to set a threshold between the very high variability found in vocalizations of *different* individuals and the very slight variability found in different vocal performances of the *same* individual. For this purpose I have calculated a "Difference Index" (DI) between pairs of vocal performances following the formula:

$$(MA_{p1} - MB_{p1})/GM_{p1} \times 100 + (MA_{p2} - MB_{p2})/GM_{p2} \times 100 \ldots\ldots + (MA_{p6} - MB_{p6})/GM_{p6} \times 100$$

where MA_{p1} = mean value of bout A for the first vocal parameter, MB_{p1} = mean value of bout B for the first vocal parameter, GM_{p1} = grand mean for the first vocal parameter of bout A and bout B. The formula is a summation of "normalized" difference between means for each vocal parameter: the resulting value weights the difference between two different vocal performances. If applied within individuals (between all calls of each owl of the 2005 study) and between individuals (some of all possible pairwise comparisons between different owls of the 2004 and 2005 studies) the resulting indexes can help to find a threshold value between these two conditions (same individual – different individual). The mean "difference index" (DI) for the same individuals is 4.5 (range 0.9/9.3; n = 30) calculated for all the possible comparisons between vocal performances of each owl recorded in the 2005 study. The DI for different individuals was calculated from 50 randomly selected pairwise comparisons of different owls recorded in the 2004/2005 studies and 6 comparisons between "most similar" owl calls. The mean DI for different individuals is 40.8 (range 15.1/72.4; n = 56). The value between the lower range of different individual (15.1) and the upper range of same individual (9.3) is 12.2. Mean DI for different owls minus two times the Standard Deviation is 13 and mean DI for same owls plus two times the SD is 8.5, therefore DI = 12 can be reasonably chosen as a threshold value.

DISCUSSION

The present study shows an interesting characteristic of Scops owl call: a consistent percentage of birds sings more than a single call type. As one can expect, an increased recording time and number of recording sessions determine an increased presence of the second call type, which sometimes does not appear in all vocal performances of the same individual. Normally there is a preferred call, which is more often sung; but in some cases, a bird can switch from one preferred call to the second in two different bouts. This is an important point to keep in mind when trying to answer the question: "does this call belong to the same owl or not?". Since some Scops owls seem to have a call repertoire (2 different call types), I think that for each owl a minimum of about 10 minutes of recording time – possibly split in 2/3 sessions – is needed to check for the presence of a different call type.

Scops owls often sing long bouts, which may last for many minutes. During these long performances, sometimes an owl may sing some hoots with a very slightly modified spectrogram. These minor changes were evaluated within the quantitative analysis of spectrograms. Some intra-individual variability was found by other authors too (Galeotti & Sacchi 2001).

The evaluation of vocal differences between individuals and vocal stability over time can be made by qualitative visual analysis of spectrograms or by quantitative methods. Although most studies rely only on quantitative methods (Christie *et al.* 2004, Aubin *et al.* 2004, Weary *et al.* 1990, Bard *et al.* 2002, Mathevon *et al.* 2003, Delport *et al.* 2002, Tripp 2004, Peake *et al.* 1998, Nelson 1989), it
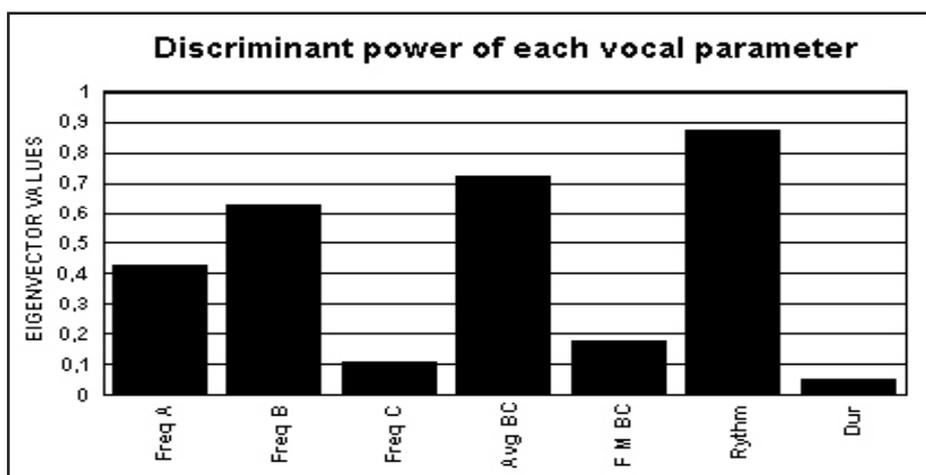

Figure 5. Eigenvector values from CVA for each acoustic measure of owl hoots.
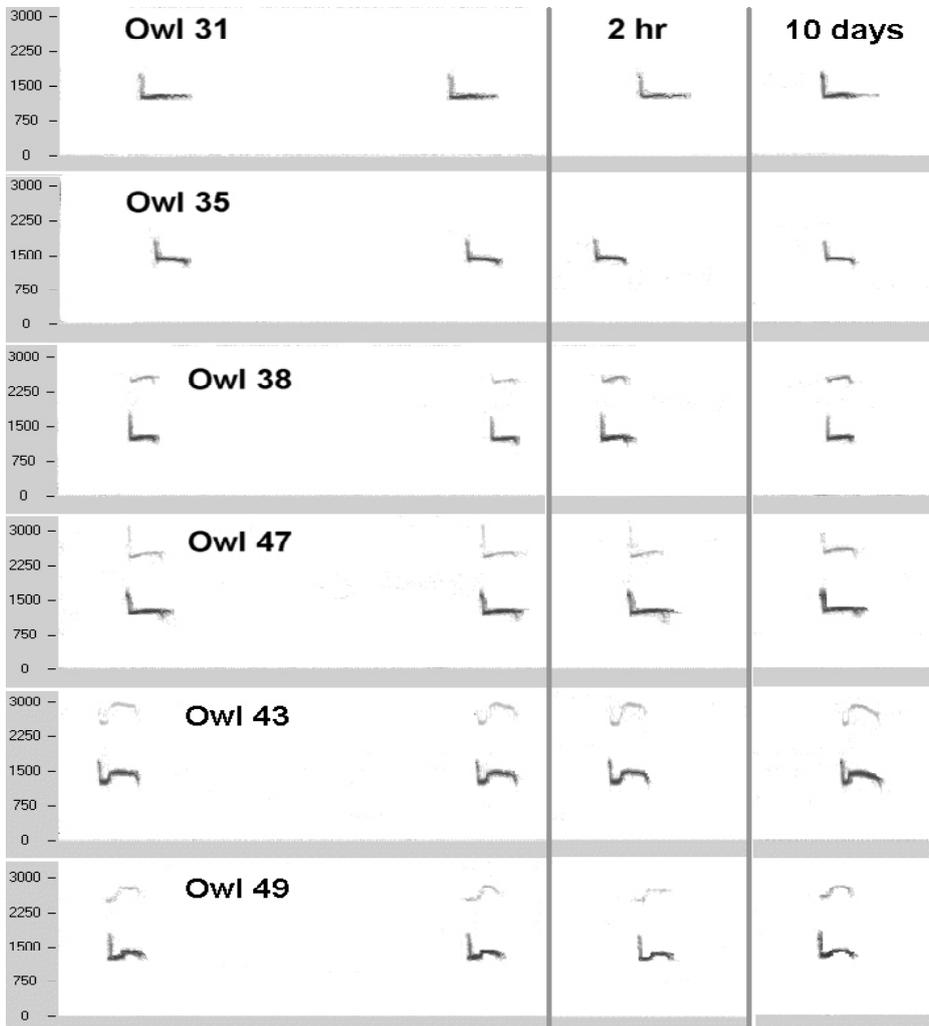
Figure 6. Spectrograms of Scops Owl recorded in 2005. Left column: baseline recording. Center column: call recorded 2 hours after baseline recording. Right column: call recorded 10 days after first recording.

is not always true that the qualitative method is less useful. Only a few studies have actually looked at how the quantitative methods perform in comparisons with human observation (Jones *et al.* 2001). Janik (1999) showed that five human observers were more likely than the quantitative computerized methods to identify signature whistles in bottlenose dolphins. Terry *et al.* (2005) point out that in most cases qualitative comparisons are used as a first level of analysis and in some cases they have proved more effective than quantitative approaches. Nevertheless, as stated by Kuntz & Stacey (1997), the
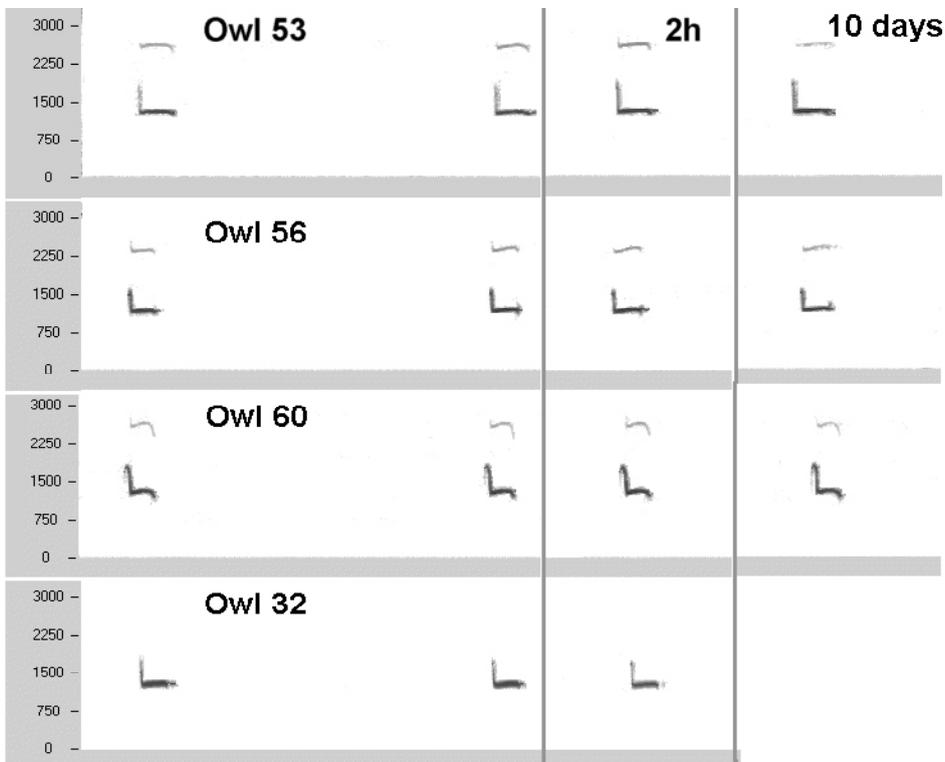
Figure 6 (continued)

visual similarity among some calls of the same species points out a major problem for discriminating individuals using spectrograms: it is unlikely that visual cues alone could separate all subjects with accuracy. In this paper I suggest a multi-approach method to recognize individual vocalization, where the visual spectrographic analysis is only the first step (necessary, but not sufficient) and must be combined with a second quantitative step. However, this study shows that the reliability of qualitative visual analysis for discriminating between different Scops owl is quite high (Figure 3). A problem – as stated above - arises when comparing very similar owl calls that need to be discriminated: in these cases the qualitative method alone may not be able to reliably identify individuals.

The results of my work show that individual differences between Scops owl spontaneous calls are striking and evident (Figure 3 and Table 1), confirming those obtained by Galeotti & Sacchi (2001) with playback stimulation. Analysis of the relative identification power of vocal parameters, shown in Table 2 and Figure 5, reveals that one temporal (Rhythm of the call) and three frequency features (Mean, Beginning of fundamental frequency and Maximum frequency) contribute strongly to individual differences, while duration and
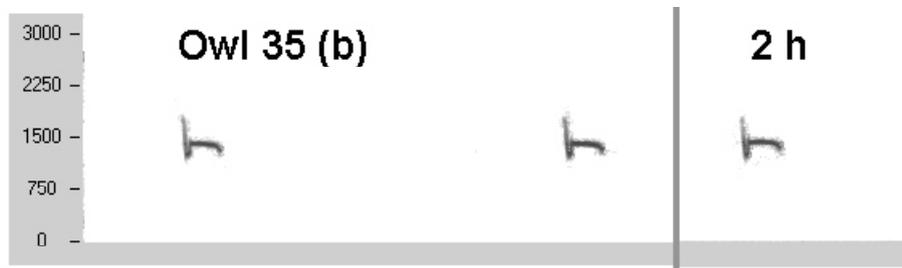
Figure 7.   Spectrograms of the second call type of owl 35 (check the first call type in Figure 6 above). Left column: first baseline recording. Right column: 2 hours after first recording.

frequency at the end of hoot are less important. These findings are dissimilar to those reported by Galeotti & Sacchi (2001), who found a lower CV_w for hoot duration, a higher CV_w for Rhythm and a lower CV_b/CV_w ratio for average fundamental frequency. This means a higher discrimination for hoot duration and a weaker discrimination for frequency, compared to that the present study. The discrepancy may be due to a different experimental protocol (playback stimulation vs spontaneous call) and/or to a different method of measurement, since I measured all temporal parameters on the oscillogram and for frequency measurements I used the *dominant* frequency values. It must be said that in my work hoot duration was sometimes affected by slight inaccuracies of measurement, due to the overlapping environmental noise (e.g. unavoidable cricket noise); this could have increased the CV_w value for that variable in the present work. However, my findings that rhythm and pitch of hoots are the best individual markers confirm earlier studies by Koenig (1973).

Call characteristics of Scops owls remain relatively constant for at least a short time (10 days during the same breeding season). Visual analysis of spectrograms of all owls shows a very constant structure and quantitative analysis by means of Friedman ANOVA reveals that 60% of owls do not change significantly their vocal parameters. This finding was similar to that reported by Galeotti & Sacchi (2001), who found a correct hoot classification rate between two recording session in the same breeding season varying from 60% to 100% in all individuals but one. Nevertheless, in the present study 40% of owls showed a statistically significant variation over time of one or two vocal parameters. Although these variations are by far less marked if compared to those between different individuals, which show very high F values and significant differences between *all* vocal features, it is clear that a certain variability between different call bouts of the same individual exists and may reach, in some cases, a statistically significant level. This slight variability between different call bouts sung over time by the same individual has been found also
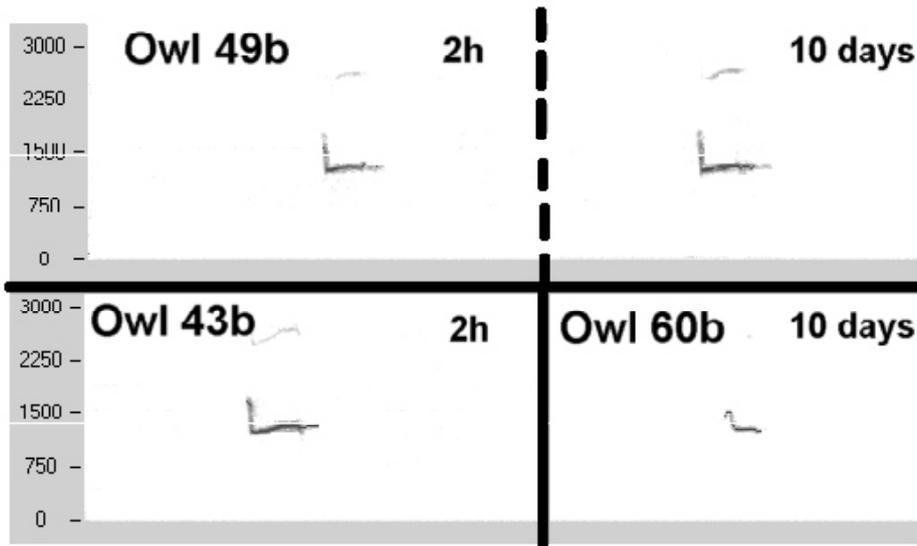
Figure 8. Spectrograms of the second call types of owl 49, 43 and 60. Owl 49 (above in figure) showed a different call type 2 hours (left) and 10 days (right) after basal recording; while owls 43 and 60 (below in figure) showed a second call type only in one recording session (after 2 hours on the left and 10 days on the right).

by other authors (Galeotti & Sacchi 2001; Delport *et al.* 2002; Tripp 2004) in different owl species. Generally the quantitative approach used by these studies is Discriminant Function Analysis (DFA), which classifies hoots and says how many hoots belong to the same individual. The percentage of correct classification varies from 100% to as low as 50%, leading to the need for a preliminary choice of threshold value. This was set at different levels (60% in Tripp 2004 or 50% in Eakle *et al.* 1989) or not explicitly declared (Galeotti & Sacchi 2001). Since the variability of the calls of the same owl over a long time (e.g. between successive breeding seasons) may be even greater (Delport *et al.* 2002; Tripp 2004), the discriminating power of this method may decrease proportionally.

In the present work I suggest a multi step qualitative/quantitative approach, with a prominent role given to the morphological analysis of spectrograms. The first step is an identification between calls of different or same individuals by means of visual qualitative analysis of spectrograms; the same spectrographic structure is a prerequisite – necessary, but not sufficient – to say that vocal samples belong to the same individual. Quantitative comparison of six acoustic features is then performed. A statistically 'not significant' result means that vocal samples are from the same bird. If a slight significant difference is found in some vocal parameters, as happened in this work, a comparison of the Difference Index with the threshold value (see above in results for DI calculation) helps to answer the question: "Are

the vocal samples from the same individual?". DI threshold value was calculated on the basis of all *within* individual pairwise comparisons in the 2005 study and a large sample of *between* individuals pairwise comparisons in 2004 and 2005. I have found that this method can reliably discriminate 13 different Scops owl calls recorded in 2004 and can individually recognize the calls in all owls recorded in 2005. However, it must be pointed out that demonstration of vocal stability over a longer time (e.g. one year) requires independent identification of individuals (Terry *et al.* 2005). This is the main criticism against my work and most of those I have cited in the references.

Further studies are needed to assess the effectiveness and usefulness of the method I have suggested, particularly long term studies comparing calls recorded one or more years apart of individually recognizable birds. Other interesting research topics concern which vocal features are actually used by the Scops owl itself to recognize conspecifics. Moreover recent studies in Zebra finches (Sturdy 2004) have shown that recognition of certain song signatures is influenced by the social context: these findings stimulate new research about the biological and ethological significance of vocal individuality in birds.

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REFERENCES

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.*, **26**, 32-46.

Appleby, B. M. & Redpath, S. M. (1997). Variation in the male territorial hoot of the Tawny owl (*Strix aluco*) in three English populations. *Ibis*, **139**, 152-158.

Aubin, T., Jouventin, P. & Hildebrand, C. (2000). Penguins use the two-voice system to recognize each other. *Proc. R. Soc. Lond. Ser. B*, **267**, 1081-1087.

Aubin, T., Mathevon, N., Da Silva, M. L., Vielliard, J. M. E. & Sebe, F. (2004). How a simple and stereotyped acoustic signal transmits individual information: the song of White-browed warbler *Basileuterus leucoblepharus*. *An. Acad. Bras. de Ciências,* **76**, 335-344.

Bard, S. C., Hau, M., Wikelski, M. & Wingfield, J. C. (2002). Vocal distinctiveness and response to conspecific playback in the Spotted antbird, a neotropical suboscine. *The Condor,* **104**, 387-394.

Brichetti, P. & Fracasso G. (2003). *Avifauna italiana. Vol. I.* A. Perdisa Editore, p. 328.

Campbell, N. A. & Atchley, W. R. (1981). The geometry of canonical variate analysis. *Systematic Zool.*, **30**, 268-280.

Catchpole, C. K. & Slater, P. J. B. (1995). *Bird Song. Biological themes and variations.* Cambridge: Cambridge University Press.

Christie, P. J., Mennill, D. J. & Ratcliffe, L. M.(2004). Chickadee song structure is

individually distinctive over long broadcasting distances. *Behaviour*, **141**, 101-124.

Cramp, S. (1985). *The birds of the Western Palearctic*. Oxford: Oxford University Press, Vol IV, p. 454-465.

Delport, W., Kemp, A. C. & Ferguson, J. W. H. (2002). Vocal identification of individual African wood owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency. *Ibis*, **144**, 30-39.

Eakle, W. L., Mannan, R. W. & Grubb, T. G. (1989). Identification of individual breeding Bald eagle by voice analysis. *J. Wild Manage.*, **53**, 450-455.

Galeotti, P. & Pavan, G. (1991). Individual recognition of male Tawny owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethol. Ecol. Evol.* **3**, 113-126.

Galeotti, P., Sacchi, R. & Perani, E. (1997). Cooperative defense and intrasexual aggression in Scops owl (*Otus scops*): responses to playback of male and female. *J. Raptor Res.* **31,** 353-357.

Galeotti, P. & Sacchi, R.(2001). Turnover of territorial Scops owl *Otus scops* as estimated by spectrographic analyses of male hoots. *J. Avian Biol.* **32**, 256-262.

Gentner, T. Q. & Hulse, S. H. (1998). Perceptual mechanisms for individual vocal recognition in European starlings, *Sturnus vulgaris*. *Anim. Behav.* **56**, 579-594.

Gentner, T. Q. (2004). Neural systems for individual song recognition in adult birds. *Ann. N.Y. Acad. Sci.*, **1016**, 282-302.

Gilbert, G., McGregor, P. K. & Tyler, G. (1994). Vocal individuality as a census tool: practical considerations illustrated by a study of two rare species. *J. Field Ornithol.*, **65**, 335-348.

Gilbert, G., Tyler, G. A. & Smith, K. W. (2002). Local annual survival of booming male Great bittern (*Botaurus stellaris*) in Britain, in the period 1990-1999. *Ibis,* **144**, 51-61.

Hammer, Ó., Harper, D. A. T. & Ryan, P. D. (2004). PAST statistical software V. 1.29 User manual., available on the Internet at: http://folk.uio.no/ohammer/past.

Haven Wiley, R. (2005). Individuality in song of Acadian flycatchers and recognition of neighbours. *Anim. Behav.* **70**, 237-247.

Janik, V. M. (1999). Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. *Anim. Behav.*, **57**, 133-143.

Jones, A. E., ten Cate, C. & Bijleveld, C. C. J. H. (2001). The inter-observer reliability of scoring sonograms by eye: a study on methods, illustrated Zebra finch songs. *Anim. Behav.*, **62**, 791-801.

Jouventin, P. & Aubin, T. (2002). Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. *Animal Behaviour,* **64**, 747-757.

Koenig, L. (1973). Das Aktionssystem der Zwergohreule *Otus scops*. *Adv. Ethol.*, **13**, 1-124.

Krebs, J. R. (1976). Habituation and song repertoire in the Great tit. *Behav. Ecol. Sociobiol.*, **1**, 215-227.

Kuntz, W. & Stacey, P. B. (February 1997). Preliminary investigation of vocal variation in the Mexican spotted owl (*Strix occidentalis lucida*): would vocal analysis of four note location call be a useful field tool for individual identification? In Biology and conservation of owls of the Northern Hemisphere. Proc. 2nd Int. Symposium. Winnipeg, Manitoba (USA)

Lengagne, T., Lauga, J. & Aubin, T. (2001). Intra-syllabic acoustic signatures used by the King penguin in parent-chick recognition: an experimental approach. *J. Exp. Biol.*, **204**, 663-672.

Lessells, C. M., Rowe, C. L. & McGregor P. K. (1995). Individual and sex differences in the provisioning calls of European bee eaters. *Anim. Behav.*, **49**, 244-247.

Lind, H., Dabelsteen, T. & McGregor, P. K. (1996). Female great tits can identify mates by song. *Anim. Behav.,* **52**, 667-671.

Lovell, S. F. & Ross Lein, M. (2004). Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behav. Ecol.*, **15**, 799-804.

Mathevon, N., Charrier, I. & Jouventin, P. (2003). Potential for individual recognition in acoustic signals: a comparative study of two gulls with different nesting patterns. *C. R. Biologies* **326**, 329-337.

McGregor, P. K. & Krebs, J. R. (1982). Song types in a population of Great tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Behaviour*, **79**, 126-152

McGregor, P. K., Anderson, C. M., Harris, J., Seal, J. R. & Soul, J. M.(1994). Individual differences in song of Fan-tailed warblers *Cisticola juncidis* in Portugal. *Airo*, **5**, 17-21.

Nelson, D. A. (1989). Song frequency as a cue for recognition of species and individuals in the Field sparrow (*Spizella pusilla*). *J. Comp. Psychol.*, **103**, 171-176.

Peake, T. M., McGregor, P. K., Smith, K. W., Tyler, G., Gilbert, G. & Green, R. E. (1998). Individuality in Corncrake *Crex crex* vocalization. *Ibis*, **140**, 120-127.

Puglisi, L. & Adamo, C. (2004). Discrimination of individual voices in male Great bitterns (*Botaurus stellaris*) in Italy. *The Auk*, **121**, 541-547

Riebel, K. & Slater, P. J. B. (2003). Temporal variation in male Chaffinch song depends on the singer and the song type. *Behaviour*, **140**, 269-288.

Sacchi, R., Perani, E. & Galeotti, P (1999). Population density and demographic trend of the Scops Owl *Otus scops* in the Northern Appennine (Oltrepò Pavese, Northern Italy). *Avocetta*, **23**, 58-64.

Scherrer, B. (1984). Biostatistique. Quebec: Gaetan Morin Press.

Searby, A., Jouventin, P. & Aubin, T.(2004). Acoustic recognition in macaroni penguins: an original signature system. *Anim. Behav.*, **67**, 615-625.

Siegel, S. (1956). Nonparametric statistic for the behavioural sciences. McGraw - Hill.

Slater, P. J. B. (1983). Sequences of song in Chaffinches. *Anim. Behav.*, **31**, 272-281.

Sturdy, C. B. (2004). A social call. *Nature*, **430**, 414.

Terry, A. M., Peake, T. M. & McGregor, P. K. (2005). The role of vocal individuality in conservation. *Frontiers in Zoology*, **2**, 10.

Tripp T. M. (2004). Use of bioacoustics for population monitoring in the Western screech-owl (*Megascops kennicottii*). MSc thesis, September 2004. University of Northern British Columbia – Canada.

Weary, D. M., Norris, K. J. & Falls, J. B. (1990). Song features birds use to identify individuals. *The Auk* **107**, 623-625.