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Do flight-calls of Redwings differ during nocturnal and diurnal migration and daytime stopovers?

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In the present study, we analyzed 173 spectrograms of acoustic signals of Redwings *Turdus iliacus*. These were issued during diurnal and nocturnal migratory flight and also during feeding, when resting and before take-off at daytime stopovers. During nocturnal and diurnal migration flights and daytime stopovers, Redwings use a single type of signal, a long *tsii*. It is classified as a species-specific attraction call. In flight Redwings emit shorter calls than during daytime stopovers. We did not find confirmation of the hypothesis that during nocturnal migration in the absence of visual contact with each other, due to low light levels and much looser flocks in the course of daytime migration, Redwings emit longer signals with wider frequency spectrum than in the daytime.

1. Introduction

Many songbirds which migrate at night give characteristic simple, species-specific flight-calls. Some fundamental features of flight-calls remain poorly known, including their functions and variability (see review: Farnsworth 2007b). In the recent years, due to technological developments and the advent of better recording and archiving techniques, acoustic monitoring of night flight-calls is increasingly used for studying species composition and numbers of nocturnally migrating birds and of the timing of their migration (Farnsworth & Russell 2007, Gagnon *et al*. 2010, Sanders & Mennill 2014, Smith *et al*. 2014). However, identification of some of the recorded sounds is difficult or impossible (Gal *et al*. 1998, Evans & Rosenberg 2000, Lanzone *et al.* 2009).

Our field studies of acoustic signalling of birds in the eastern part of Gulf of Finland and on the Courish Spit of the Baltic Sea showed that nocturnal flight-calls of passerines are by ear virtually indistinguishable from their diurnal "species-specific attraction calls" (Bolshakov 1975, 1977, 1997, Bolshakov *et al*. 2002). More recent studies in North America also showed that night flight-calls recorded during migratory periods in *Catharus* thrushes and many wood warblers (Parulidae) were also present in their acoustic repertoires outside of the migratory period (Evans 1994, Farnsworth 2007a, 2007b, Lanzone *et al.* 2009). Detection by ear or by analysing spectrograms of signals of unknown origin is explained by at least three reasons: 1) poor knowledge of acoustic repertoires in some species (Lanzone *et al.* 2009); 2) the fact that spectrograms of some species' night flight-calls often show very high similarity or exhibit extensive variability, making them difficult to distinguish from other species (Evans & Rosenberg 2000); 3) birds emit, at night, only fragments of their normal signals. In some cases, even a concilium of experienced field ornithologists may fail to identify the species which emitted a recorded signal (Gal *et al.* 1998).

Here we present the results of the analysis of calls issued during the migratory period by Redwings (*Turdus iliacus*). The Redwing in the Baltic region is a common nocturnal migrant, but also migrates in the daytime. A characteristic feature of their behaviour is to emit sound signals, both in the daytime and at night (Bergmann & Helb 1982, Snow & Perrins 1998). Compared with the numerous Song Thrushes (*T. philomelos*), Redwings are more social. Members of this species during the day often migrate and feed at stopovers in large flocks (Bolshakov *et al.* 2002). The main aim of our work was to define the duration and frequency characteristics of their diurnal and nocturnal flight-calls, to look for differences between them.

Unlike daily migratory flights, during night migration Redwings have no visual contacts and fly at a great distance from each other. If during night flight the signalization for Redwings has such important functions as maintaining flock structure, stimulating conspecifics, coordinating movements, or some combination of these (Hamilton 1962, Evans & O'Brien 2002, Farnsworth 2007b), it should be expected that at night they will produce longer signals with wider frequency spectrum than in the daytime. Such signals give more opportunities for orientation in space and can be heard at a greater distance. Another goal was to compare the structure, timing and frequency characteristics of flight-calls of Redwings with their species-specific attraction calls, which they issued at daytime stopovers, to make sure that the Redwings in all cases use the same species-specific type signals.

2. Material and methods

This study is based on long-term recordings of audio signals given by Redwings during night and day migration flight in the eastern part of Gulf of Finland near Lisiy Nos settlement (11 km west of St. Petersburg) and at the Biological Station Rybachy on the Courish Spit of the Baltic Sea (55°09'N, 20°51'E) in autumn seasons. For daytime we also analysed records with calls of Redwings made here in autumn during their daytime stopovers. Records of nocturnal flight-calls were made in the middle of the night, and diurnal flight-calls – in the first two hours after sunrise. Species-specific signals of Redwings during the feeding and resting on daytime stopovers were recorded in the middle and the end of the day, and before the beginning of the nocturnal take-off – in the first 40 minutes after sunset.

All recordings of Redwing voices at night and in the daytime were made by the same tape recorder UHER 4000 REPORT-L (UHER Werke GmbH München), equipped with a 24" Grampian parabolic reflector with DP6 omnidirectional dynamic microphone (frequency response 200–15,000 Hz; Grampian Reproducers Ltd, London). Signal recording from nocturnally flying birds was performed over an area illuminated with white light and in the area of the strip of white light from horizontally aimed searchlights (Bolshakov *et al.* 2002).

In both situations a layer of air lit up to a height of about 100 m made it possible to see the flying birds and to identify them by their silhouettes and signals. Recording signals from diurnally flying birds was also carried out at flight altitudes up to *ca*. 100 m a.g.l. During the observations, we directed the parabolic reflector towards flying thrushes and recorded their signals until they disappeared out of sight. After each recording, the observer noted the date, time, flight altitude of the birds estimated by eye, and weather (cloud, wind, rainfall). For the recordings of calls of Redwings at daytime stopovers, the observer noted the date, time, distance to the birds, the weather, and also in what situation (feeding, resting, before the beginning of the nocturnal take-off) they were made.

From a large number of records with Redwing calls for the analysis we have chosen only those calls which, first, were recorded in calm weather with and no precipitation, and second, when birds flew at a height of 20–50 m, or sat at a distance 20–50 m from the observer. This allowed us to reduce the noise effects caused by differences in weather conditions and the possible distortion in the signals due to varying distance from the microphone to the bird (see Horton *et al.* 2015). In total, we analyzed 62 calls of nocturnally flying Redwings and 34 calls from Redwings engaged in diurnal migratory flights. The number of reviewed Redwing species-specific attraction calls that were recorded at daytime stopovers during feeding, rest and be-

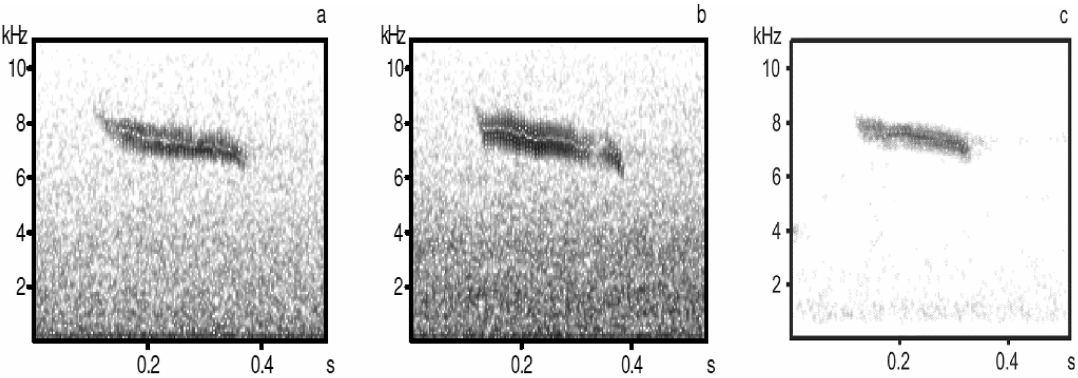

Fig. 1. Samples of typical spectrograms of Redwing calls during nocturnal flight (a), during diurnal flight (b) and at daytime stopover (c). The vertical axis is the frequency in kHz; the horizontal axis is the duration, in s.

fore the beginning of the nocturnal take-off was 77.

We visualized selected calls as sound spectrograms with Cool Edit Pro 2 software within a frequency range of 21–22,050 Hz (spectral settings: 2,048 and 8,192 FFT size, Blackman-Harris window), sample rate 22,050 Hz with 16 bit depth. In spectrograms many signals of Redwings recorded during their migratory flight and at stopovers looked similar (Fig. 1). However, they differed in the presence or absence of high-frequency peak (Fhp) at the beginning and low-frequency peak (Flp) at the end of the signal, different rate of frequency modulation, signal duration and structural changes caused both by individual variation and also by signal degradation due to various environments. The peaks at the beginning and (or) at the end of the signals were recorded less than 30% of the spectrograms. To assess the variation in the spectrograms between groups of birds we using the visual inspection ignored presence of these peaks and focused attention on the "body" of signal where the main energy was concentrated.

Here we manually made the following temporal and spectral measurements with the cursor: 1) signal duration; 2) maximum frequency in the beginning (F1) and in the end of the signal (F2); 3) minimum frequency in the beginning (F3) and in the end of the signal (F4). This set of features was a subset of those based on ACUSTAT (Fristrup & Watkins 1995). Based on these frequency measurements, we further calculated the frequency band in the beginning (F1–F3) and in the end of the signal (F2–F4), changing the maximum (F1–F2) and minimum frequency (F3–F4) from the beginning to the end of the signal. All measurements were made by the same person (M.E.). All data met the assumptions of normality (Kolmogorov-Smirnov test, $P > 0.05$).

To test for significance of differences between mean values of variables for calls of three groups (night flight-calls, daytime flight-calls and species-specific calls at stopovers) we used the one-way ANOVAs for each variable, using a Bonferroni correction (a = 0.017) to correct for multiple tests and to reduce the likelihood of type 1 errors. We also applied stepwise discriminant function analysis (DFA) to determine which signal measurements were the best discriminators of groups of nocturnal and diurnal signals and what classification success rate they provide in group identification. Since a high-frequency peak at the beginning of the signal and low-frequency peak at the end of the signal were recorded on spectrograms only a small proportion of the birds, these variables were not included in the DFA. We set the probability for entering the predictors at 0.05 and the probability for removing them at 0.10.

3. Results

Direct observations show that both during nocturnal migration and during diurnal migration flights, Redwings used a single call type which can be given as *tsii*. By ear, *tsii* signals given under these circumstances do not differ from their species-specific calls, recorded at stopover during feeding, rest and before night take-off.

Table 1. Range and mean values (± SD) of spectral and temporal measurements of Redwing calls recorded during nocturnal and migration flight, and species-specific calls recorded at daytime stopovers

Signal variable	Nocturnal flight-calls	Daytime flight-calls	Species-specific calls at daytime stopovers	ANOVA
Fhp, kHz	8.36 ± 0.35 (*n* = 12) 7.71–8.90	8.59 ± 0.33 (*n* = 8) 7.88–9.02	8.57 ± 0.38 (*n* = 32) 7.64–9.15	$F_{2, 51}$ = 1.59, *p* = 0.215
Flp, kHz	5.98 ± 0.47 (*n* = 10) 5.21–6.72	5.86 ± 0.33 (*n* = 16) 5.12–6.65	5.79 ± 0.33 (*n* = 20) 5.10–6.35	$F_{2, 47}$ = 0.96, *p* = 0.391
F1, kHz	7.96 ± 0.46 (*n* = 62) 6.81–8.77	8.06 ± 0.30 (*n* = 34) 7.57–8.74	7.96 ± 0.34 (*n* = 77) 7.13–8.90	$F_{2, 170}$ = 0.89, *p* = 0.411
F2, kHz	7.11 ± 0.41 (*n* = 62) 6.08–7.90	7.40 ± 0.34 (*n* = 34) 6.59–7.99	7.25 ± 0.24 (*n* = 77) 6.81–7.79	$F_{2, 170}$ = 8.24, *p* < 0.001
F3, kHz	7.17 ± 0.36 (*n* = 62) 6.22–8.07	6.96 ± 0.43 (*n* = 34) 4.99–7.60	6.92 ± 0.38 (*n* = 77) 5.65–7.61	$F_{2, 170}$ = 7.58, *p* = 0.001
F4, kHz	6.29 ± 0.31 (*n* = 62) 5.42–6.94	6.22 ± 0.27 (*n* = 34) 5.68–6.70	6.14 ± 0.30 (*n* = 77) 5.38–6.69	$F_{2, 170}$ = 4.23, *p* = 0.017
F1–F3, kHz	0.80 ± 0.24 (*n* = 62) 0.33–1.61	1.11 ± 0.41 (*n* = 34) 0.65–2.84	1.04 ± 0.30 (*n* = 77) 0.47–1.93	$F_{2, 170}$ = 14.69, *p* < 0.001
F2–F4, kHz	0.83 ± 0.29 (*n* = 62) 0.30–1.65	x = 1.18 ± 0.26 (*n* = 34) 0.55–1.55	x = 1.11 ±0.26 (*n* = 77) 0.51–1.81	$F_{2, 170}$ = 26.19, *p* < 0.001
F1–F2, kHz	0.86 ± 0.29 (*n* = 62) 0.29–1.73	0.66 ± 0.37 (*n* = 34) –0.14–1.42	0.71 ± 0.33 (*n* = 77) 0.09–1.69	$F_{2, 170}$ = 5.04, *p* = 0.007
F3–F4, kHz	0.89 ± 0.23 (*n* = 62) 0.27–1.31	0.74 ± 0.49 (*n* = 34) –1.09–1.78	0.79 ± 0.41 (*n* = 77) –0.32–1.87	$F_{2, 170}$ = 1.95, *p* = 0.145
Duration, ms	281 ± 49 (*n* = 62) 161–387	252 ± 55 (*n* = 34) 131–348	319 ± 66 (*n* = 77) 187–473	$F_{2, 170}$ = 16.83, *p* < 0.001

According to the spectral measurements of these signals on spectrograms their frequency spectrum was within the limits of 5.10–9.15 kHz. Such a large range between the minimum and maximum frequency boundaries was due to the marginal values of the high-frequency peak at the beginning and the low-frequency peak at the end of some signals. In many cases the extreme limits of frequency spectrum range for each individual signal were significantly smaller. In the presence of both peaks, they varied on average from 5.8 to 8.6 kHz, and in the absence of these peaks, on average from 6.1 to 8.1 kHz. The sizes of both high-frequency and low-frequency peak on those few nightly and daytime flight-calls, and species-specific calls on average did not differ significantly (Table 1). Comparison of other spectral and temporal measurements in these signals, as well as in those signals where there were no peaks, showed the following differences between night and daytime flight-calls and species-specific calls at stopovers (Table 1, 2).

Table 2. Post hoc pairwise comparisons of mean values of the individual spectral and temporal measurements of Redwing calls recorded during nocturnal and daytime migration flight, and species-specific calls recorded at daytime stopovers. For post-hoc tests, the *P*-values are given after Bonferroni corrections. The level of significance was set at $P < 0.017$. The results are shown only for comparisons with significant effects.

Signal variable	Comparisons	*p*
F2	Nocturnal flight-calls vs diurnal flight-calls	< 0.001
F3	Nocturnal flight-calls vs calls during daytime stopovers	0.001
F4	Nocturnal flight-calls vs calls during daytime stopovers	0.013
F1–F3	Nocturnal flight-calls vs diurnal flight-calls	< 0.001
	Nocturnal flight-calls vs calls during daytime stopovers	< 0.001
F2–F4	Nocturnal flight-calls vs diurnal flight-calls	< 0.001
	Nocturnal flight-calls vs calls during daytime stopovers	< 0.001
Duration	Nocturnal flight-calls vs calls during daytime stopovers	0.001
	Diurnal flight-calls vs calls during daytime stopovers	< 0.001

1. Nocturnal flight-calls had on average a significantly smaller frequency width (F1–F3, F2–F4) than diurnal flight-calls and daytime species-specific calls at stops.
2. The average duration of nocturnal flight-calls was significantly less than for daytime species-specific calls at stops.
3. Significant differences in spectral and temporal measurements between daytime flight-calls and species-specific calls at stops were found only in the duration of the signals: the birds migrating in the day emitted on average shorter signals than during the stops.

We performed DFA using all spectral and temporal measurements, except those related to the high-frequency peak at the beginning of the signal and low-frequency peak at the end of the signal. Almost all spectral measurements included in the analysis were significantly correlated. As the strongest correlation coefficient was 0.64, we consider multicollinearity to have been a minor problem in DFA. Three variables, signal duration, frequency band in the end of the signal (F2–F4) and the minimum frequency in the beginning of the signal (F3) were retained in the model in DFA by stepwise analysis (canonical correlation = 0.547, Wilks' Lambda = 0.587, $\chi^2 = 88.34$, $df = 6$, $p = 0.0003$). DFA based on these variables showed 62.4% classification success. The function correctly classified 73% of 62 nocturnal flight-calls, 59% of 34 of diurnal flight-calls and 55% of 77 of species-specific calls at stopovers. Results of the DFA show that identifying groups of Redwing signals (e.g. nocturnal flight-calls, diurnal flight-calls and species-specific calls during daytime stopovers) by individual signal variables is practically impossible.

4. Discussion

Analysis of spectrograms of Redwing flight-calls recorded during nocturnal and diurnal migration, and species-specific calls recorded at stopovers showed that in many cases they had a rather simple structure (Fig. 1). In all three groups of thrushes one could see the high-frequency peak at the beginning of the signal and (or) low-frequency peak at the end of the signal on some spectrograms. The presence or absence of these peaks may have been due to both individual differences in the structure of the bird's voice and structural changes in the signal as a result of differences in the distance between the bird and the microphone. Comparing the spectrograms of nocturnal and diurnal flight-calls from Redwings, migrating at altitudes of 20–100 m, we found that the proportion of calls with peaks and also the duration and frequency bandwidth of the signals has significantly decreased (unpublished data). This could be due to a progressive change in the structure of signals during its propagation in air. It is known that with increasing distance from the source of its origin, the signal is attenuated, especially in the high-frequency part more susceptible to absorption and scattering in the air, accumulates reverberation and amplitude modulation rate (Naguib & Wiley 2001). In order to minimize the effect of signal degradation due to variation in distance, and to be able to compare signals with and without peaks, first, we limited the analysis of spectrograms to only the records made at a fixed distance from the microphone to flying or seated birds (see Methods). Second, we focused on spectral and temporal measurements of the signal's "body" which was most suitable for estimating the differences between separate groups of signals.

During their seasonal migrations Redwings are social in the daytime. They gather in flocks when feeding at stopovers and during daytime flights. At night, flying in flocks similar to the daytime pattern is observed only when they depart soon after sunset. However, these flocks disintegrate after darkness. At night, even if flocks exist, they are very loose groups in which the distance between individual birds is of dozens and hundreds of metres (Bolshakov *et al.* 2002). We assumed that during nocturnal migration in the absence of visual contact with each other, due to low light levels and much looser flocks than during daytime migration, Redwings should emit longer signals with wider frequency spectrum than in the daytime. Extending the frequency spectrum of the signal through low frequencies could allow birds to transmit information across longer distances, while higher signal frequencies could enable birds to better determine the distance to the sound source (Marten & Marler 1977, Roberts *et al.* 1981, Larom *et al.* 1997, Larom 2002, Venuto & Teylor 2002).

Comparing time and spectral measurements of the night and day flight-calls of Redwings, we did not find support for any of our assumptions. Although night calls were on average longer than daytime calls, these differences were not statistically significant. As for the width of the frequency spectrum of flight-calls, contrary to our expectations, in nocturnal calls it was even smaller than in diurnal ones (Table 1, 2). The question remains whether decreasing amplitude of the signal was a response to its increasing duration, or it was caused by different ambient conditions during day and night (temperature and humidity of air; see Horton *et al.* 2015). Sounds travel greater distances at night than during the day (Larom 2002, Rundus & Hart 2002). When comparing temporal and spectral characteristics of day flight-calls of Redwings with the similar data of species-specific calls at stopovers, we found significant differences only in the length of the signal. Stopover calls of Redwings were much longer than diurnal flight-calls, and also longer than nocturnal flight-calls (Table 1, 2).

We speculated, but reasons for longer signals at stopovers may be that during stopovers birds are more prone to emotional and (or) stress factors when interacting with each other and the environment, than during the flight. Signals emitted at stopovers, apart from the communicative function, can also carry additional information. It is also possible that it is physically more difficult (or impossible) to emit long signals during the flight than when the birds are perched on bushes, trees or on the ground.

Stepwise discriminant function analysis selected signal duration, minimum frequency in the beginning of the signal and frequency band in the end of the signal as the best discriminators of groups of nocturnal and diurnal calls. The discriminant function based on these three measurements correctly classified 73% of night flight-calls, 59% of day flight-calls and 55% of species-specific calls at stopovers, which gives the overall classification success of 62%. Such low success in identification of call groups by discriminant analysis of spectral and temporal measurements suggests that Redwings use a single type of signal, a long *tsii*, which can be attributed to species-specific attraction calls. These calls can vary in different situations depending on (1) degree of structure degradation during its propagation in the air as a function of distance to the sound source (Naguib & Wiley 2001, Horton *et al.* 2015); (2) weather conditions during the flight (Hüppop & Hilgerloh 2012, Horton *et al.* 2015) and (3) function they carry out and (or) information they contain. Our data show that Redwings, as well as apparently many other species of nocturnal migrants, have no specialised migratory acoustic signals (Bolshakov 1975, 1977, 1997, Evans 1994, Bolshakov *et al.* 2002, 2017, Farnsworth 2007a, 2007b).

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Muuttavien punakylkirastaiden kutsuäänet

Tutkimuksessa analysoitiin punakylkirastaan (*Turdus iliacus*) spektrogrammeja päivä- ja yömuuton aikana, sekä muuton välilaskun aikana. Punakylkirastaat käyttivät vain yhden tyyppistä signaalia, pitkää ”*tsii*”-ääntä, muutonaikaisessa lennossa, sekä päivällä että yöllä. Se toimii oletettavasti lajispesifinä kutsuäänenä. Lentäessään punakylkirastaaiden kutsuääni on lyhyempi kuin muuton välilaskun aikana. Testasimme myös hypoteesia, jonka mukaan yömuuttavat punakylkirastaat hyötyisivät pidempien ja laajemman frekvenssin äänien käyttämisestä päivämuuttajiin verrattuna, koska yöaikaan valoa on vähemmän ja parvet harvempia. Tuloksemme eivät kuitenkaan tukeneet tätä hypoteesia.

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