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Vocal mimicry in the song of the icterine warbler, *Hippolais icterina* (Sylviidae, Passeriformes)

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Abstract. We recorded and analysed the songs of ten male icterine warblers (*Hippolais icterina*) in České Budějovice (Czech Republic) to identify mimicry. Imitations represented 76.2 % of the total time of all songs and we detected 42 mimicked species. Barn swallow (*Hirundo rustica*), blackbird (*Turdus merula*), common kestrel (*Falco tinnunculus*) and fieldfare (*Turdus pilaris*) were the most common species imitated. Principal components analysis (PCA) detected individual variability in the species mimicked. The length of recording needed to detect 95 % of species mimicked was assessed to be 8.2 minutes.

Key words: song variability

Introduction

The vocal mimicry is a well-known phenomenon in the song of many bird species. In addition to passerines (Passeriformes), where mimicry is most common (15-20 % of all species, Marshall 1950, Vernon 1973), there is evidence for mimicry in parrots and cuckoos too (Kelley et al. 2008). Mimickers can include in their repertoire not only the mimicry of songs and calls of other bird species, but also other sounds present in the environment. Recently, several studies concerning the learning of mimicry and its potential function have been carried out and several hypotheses have been proposed (reviewed by Kelley et al. 2008). All of them posit an adaptive value of mimicry except for one: the learning mistake hypothesis. This supposes that mimicries are the result of an accumulation of mistakes during song learning and have no specific function (Hindmarsh 1986). Mimickers should therefore learn simple and common sounds present in their environment and use them frequently in inappropriate contexts.

Song of mimickers differs considerably in the number of species mimicked and in the time spent on mimicry. For example, the vesper sparrow (*Pooecetes gramineus*) mimics rarely, probably as a result of isolation from singing conspecifics (Kroodsma 1972). Mimicry in European starlings (*Sturnus vulgaris*), although highly noticeable, represents on average only 7 % of its song bout, in addition to this 33 % of imitations are given as single calls between song bouts (Hindmarsh 1984). On the other hand, vocal mimicry may outweigh species specific parts of the song in other species. In the white-eyed vireo (*Vireo griseus*) 53 % of notes are vocal mimicry (Adkisson & Connor 1978). The song of the marsh warbler (*Acrocephalus palustris*) and that of both species of lyrebird (*Menura novaehollandiae* and *M. alberti*) are extremes that consist almost entirely of mimicry (Robinson 1974, Dowsett-Lemaire 1979). The number of species mimicked in the mimickers' song may also be variable: black-browed reed-warbler (*Acrocephalus bistrigiceps*) – eight species in the song of 13 males, European starling – 21 species in the song of 35 males, contrary to marsh warbler – 212 species in the song of 30 males (Dowsett-Lemaire 1979, Hindmarsh 1984, Hamao & Eda-Fujiwara 2004).

The icterine warbler is another European species well known for its ability to mimic. Its song is vigorous, variable and far-carrying. It consists of musical, harsh and strident sounds. It recalls the song of the marsh warbler but is more powerful. There is considerable individual variation in tunefulness (Benson 1897) and presumably to some extent in the diversity of species mimicked (Malchevski & Pukinski 1983, Cramp 1992). Malchevski & Pukinski (1983) emphasize prevalence of call mimicry in contrast to song mimicry, which is in

concordance with the results obtained by Akkermann (2006). The song of icterine warblers is highly vocal at the start of breeding season but much reduced after pair-formation. Short-term inclement weather has little effect on song intensity (Cramp 1992).

Currently, there are few studies describing song mimicry repertoire of this common species. Previously published data were not statistically analyzed and the authors simply showed the checklists of mimicked species (Malchevski & Pukinski 1983, Cramp 1992, Akkermann 2006). The aim of this paper is to (1) assess the range of mimicked species in the song of ten individual of icterine warblers, (2) estimate minimum recording length necessary to cover 95 % of species mimicked in the song, which is important information for future research on individual variability of song mimicry, and (3) determine individual song variability.

Material and Methods

Fieldwork

Fieldwork was carried out during the three breeding seasons, from April to July 2007-2009. The research was conducted in České Budějovice (Southern Bohemia), where icterine warblers occupy parks and other urban green areas (Prkna 1997).

Bird trapping was carried out from the end of April until the end of May following the methodology of Cibulková (1993). Birds were attracted by playback songs and caught using mist nets. Almost all birds caught were males (95.7 %). Each individual was ringed with an aluminium ring and a unique combination of coloured plastic rings for later identification during song recording. In total, we caught and ringed 45 males (2007 – 11 males, 2008 – 21 males, 2009 – 13 males).

Colour ringed birds were identified and their song was recorded with a digital minidisk recorder MZ-RH1, Hi-MD and a Sony ECM-T6 microphone with a plastic reflector (diameter 18 cm) placed on a 0.7 m long rod. Most of the recordings (70 %) were taken in the morning between 6 and 11 a.m. during May and June, the remaining 30 % were recorded in the afternoon during this period or at the end of April. Recordings were obtained at least two days after the bird was caught. Length of recordings ranged from 20 to 40 minutes. In total, we recorded the song of ten males.

Song analyses

We analysed ten song recordings of ten males (in the year 2007 – 1 male, 2008 – 8 males, 2009 – 1 male). We used Software RAVEN Lite 1.0 (Cornell Lab of Ornithology Ithaca, NY, USA) for partitioning the recorded songs into mimicry and species specific song parts according to the visual appearance of spectrograms and hearing control. Song mimicries were identified by acoustic comparison of these parts of the icterine warbler's song with professional song recordings of Czech avifauna (Schulze & Dingler 2003). Identification was made by the first author that has good experiences with Czech bird sounds. Parts that were not determined by the first author were listened and determined by the second author. Each identified sequence (mimicry or species specific song of icterine warbler) was given a specific code, which was used whenever this sequence appeared in the song of any analysed individual. Some sequences were not identified (9.21 %). In total, we analysed 14081 sequences (mean ± SD; 1408 ± 426 per recording). Each song was divided into: (1) icterine warbler species specific parts, (2) sequences containing mimicry and (3) unidentified sequences (including mechanical sounds and sequences that probably belonged to an exotic bird species). For each sequence type, we recorded total length (s), its proportion in relation to the total length of all songs (%), mean length and mean frequency of occurrence.

Data analyses

The length of recording necessary to cover 95 % of species mimicked was estimated by cumulative curves of the number of species mimicked in relation to total record length for each of the ten individuals. However, the song recording of each bird was not one continuous track due to other bird activities. Therefore, one recording consisted of more tracks (4.0 ± 1.0) within one visit in the territory. So a final cumulative curve for each individual was constructed as the mean cumulative curve from all relevant tracks. For each cumulative curve, we recorded the time when the song reached 95 % of bird species mimicked.

We used principal components analysis (PCA) (Software Canoco for Windows 4.5., Šmilauer 1992, ter Braak & Šmilauer 1998) to quantify the variability of the icterine warblers' song. We used the ten analysed males as "samples" and mimicked species as "species". The data unit was represented as percentages of time spent mimicking one species relative to the total length of the song recording. The percentages were log-transformed.

Results

Sequences of mimicked species represented 76.2 % of the total time of all songs. In total, we identified 42 bird species in the songs of ten males (27 ± 5 species

Table 1. *Main characteristics for mimicked species songs, species-specific songs and unidentified sequences in recordings of ten icterine warbler males.*

Order	Family	Species	% of total time	Mean length of the sequence ± SD [s]	Mean frequency of the sequence ± SD [s^{-1}]	Total time spent by imitation [s]
Passeriformes	Sylviidae	*Hippolais icterina*	14.78	0.94 ± 0.22	0.1675 ± 0.0437	1472.2
Unidet.			9.21	0.76 ± 0.17	0.1175 ± 0.0286	917.6
Falconiformes	Falconidae	*Falco tinnunculus*	8.25	1.04 ± 0.37	0.0834 ± 0.0268	822.4
Galliformes	Phasianidae	*Coturnix coturnix*	1.01	0.26 ± 0.06	0.0288 ± 0.0205	100.2
Charadriiformes	Sternidae	*Sterna hirundo*	0.16	0.24 ± 0.14	0.0038 ± 0.0119	15.5
Columbiformes	Columbidae	*Streptopelia decaocto*	1.61	1.01 ± 0.67	0.0155 ± 0.0099	160.6
Piciformes	Picidae	*Picus viridis*	0.10	0.05 ± 0.00	0.0017 ± 0.0000	9.8
		Dendrocopos major	0.08	0.17 ± 0.00	0.0004 ± 0.0000	8.4
		Jynx torquilla	0.01	0.10 ± 0.00	0.0001 ± 0.0000	1.0
Passeriformes	Alaudidae	*Alauda arvensis*	0.67	0.78 ± 0.74	0.0093 ± 0.0086	66.5
		Galerida cristata	0.47	0.31 ± 0.19	0.0051 ± 0.0173	46.6
	Hirundinidae	*Hirundo rustica*	7.53	0.68 ± 0.22	0.1186 ± 0.0275	750.0
		Delichon urbica	0.42	0.49 ± 0.48	0.0062 ± 0.0067	42.0
	Motacillidae	*Motacilla alba*	1.13	0.60 ± 0.54	0.018 ± 0.0018	113.0
	Laniidae	*Lanius collurio*	0.18	0.16 ± 0.00	0.0008 ± 0.0000	18.0
	Sylviidae	*Acrocephalus palustris*	5.11	1.41 ± 0.54	0.0342 ± 0.0172	509.0
		Sylvia atricapilla/borin	4.62	1.55 ± 0.80	0.0326 ± 0.0109	460.3
		Phylloscopus trochilus	0.97	0.81 ± 0.31	0.0126 ± 0.0088	96.5
		Sylvia atricapilla	0.78	1.65 ± 3.18	0.0023 ± 0.0021	77.8
		Acrocephalus scirpaceus	0.21	0.12 ± 0.15	0.0023 ± 0.0118	20.9
	Turdidae	*Turdus pilaris*	7.30	1.52 ± 0.52	0.0495 ± 0.0186	727.1
		Turdus merula	6.72	0.65 ± 0.12	0.1041 ± 0.0292	669.7
		Erithacus rubecula	1.50	0.77 ± 0.76	0.0154 ± 0.0251	149.4
		Turdus philomelos	1.03	0.97 ± 1.26	0.0082 ± 0.0058	102.9
		Turdus	0.79	0.94 ± 1.18	0.0069 ± 0.0065	78.8
		Phoenicurus sp.	0.66	0.31 ± 0.51	0.0063 ± 0.0154	66.1
		Luscinia megarhynchos	0.02	0.06 ± 0.00	0.0003 ± 0.0000	1.8
		Turdidae unidet.	0.11	0.21 ± 0.18	0.0017 ± 0.0029	10.6
	Remizidae	*Remiz pendulinus*	0.26	0.45 ± 0.23	0.0037 ± 0.0037	26.0
	Paridae	*Parus major*	2.66	0.55 ± 0.28	0.0421 ± 0.0136	264.9
		Cyanistes caeruleus	0.72	0.47 ± 0.57	0.0208 ± 0.0201	72.0
		Poecile palustris	0.31	0.31 ± 0.23	0.0047 ± 0.0118	30.5
		Paridae unidet.	4.82	0.83 ± 0.19	0.0553 ± 0.0170	480.1
	Sittidae	*Sitta europaea*	0.69	0.29 ± 0.27	0.0159 ± 0.0088	69.0
	Fringillidae	*Loxia curvirostra*	1.56	0.80 ± 0.25	0.0210 ± 0.0135	155.8
		Carduelis carduelis	1.22	1.60 ± 1.62	0.0097 ± 0.0085	121.1
		Carduelis chloris	0.68	0.50 ± 0.55	0.0109 ± 0.0057	67.7
		Carduelis cannabina	0.58	0.25 ± 0.17	0.0083 ± 0.0145	57.4
		Fringilla coelebs	0.40	0.21 ± 0.06	0.0128 ± 0.0104	39.8
		Coccothraustes coccothraustes	0.27	0.18 ± 0.24	0.0081 ± 0.0107	27.0
		Carduelis spinus	0.23	0.46 ± 1.04	0.0022 ± 0.0038	23.4
		Serinus serinus	0.07	0.28 ± 0.12	0.0007 ± 0.0034	6.8
		Fringillidae	0.29	0.52 ± 0.61	0.0026 ± 0.0081	28.7
	Passeridae	*Passer domesticus*	1.47	0.33 ± 0.09	0.0354 ± 0.0189	146.9
		Passer montanus	1.46	0.50 ± 0.16	0.0225 ± 0.0153	145.3
		Passer sp.	0.88	0.37 ± 0.04	0.0227 ± 0.0249	87.5
	Sturnidae	*Sturnus vulgaris*	2.19	0.76 ± 0.39	0.0294 ± 0.0135	218.7
	Corvidae	*Pica pica*	2.77	0.84 ± 0.35	0.0369 ± 0.0163	276.1
		Corvus monedula	0.99	0.90 ± 0.81	0.0114 ± 0.0087	98.8
		Garrulus glandarius	0.05	0.05 ± 0.00	0.0009 ± 0.0000	4.5
		Corvidae unidet.	0.01	0.03 ± 0.00	0.0004 ± 0.0000	1.2

per male, range from 15 to 32 species per male) (Table 1). Species mimicked belonged to six bird orders (Table 2), the majority (83.3 %) of which was formed by passerines.

Lists of the ten most common species mimicked by frequency and by proportion of time spent on mimicking them were 80 % identical, but the ranking of mimicked species differed (Table 3, examples of spectrograms Fig. 1). The five most often mimicked species based on proportion of time (%) were: common kestrel (*Falco tinnunculus*), barn swallow (*Hirundo rustica*), fieldfare (*Turdus pilaris*), blackbird (*Turdus merula*), marsh warbler (*Acrocephalus palustris*). The five most frequently mimicked were: barn swallow, blackbird, common kestrel, fieldfare and great tit (*Parus major*).

Songs probably belonging to exotic birds made up only 0.15 % of the total time and were not further inspected. One sequence was identified as a mechanical sound (resembled gambling machine) making up 0.05 % of the total time of all songs. Icterine warbler species specific song and call represented 14.78 % of the total time. Mean length of a sequence was 0.94 ± 0.22 s and mean frequency 0.1675 ± 0.0437s^{-1} (Table 1). We found 34 species specific sequences in the song of ten males. These sequences were present in the songs of almost all individuals and acoustic and

Table 2. *Taxonomic spectrum of mimicked species.*

Avian order	% of time spent by imitation	Number of species
Passeriformes	85.2	35
Falconiformes	10.9	1
Columbiformes	2.1	1
Galliformes	1.3	1
Charadriiformes	0.2	1
Piciformes	0.3	3

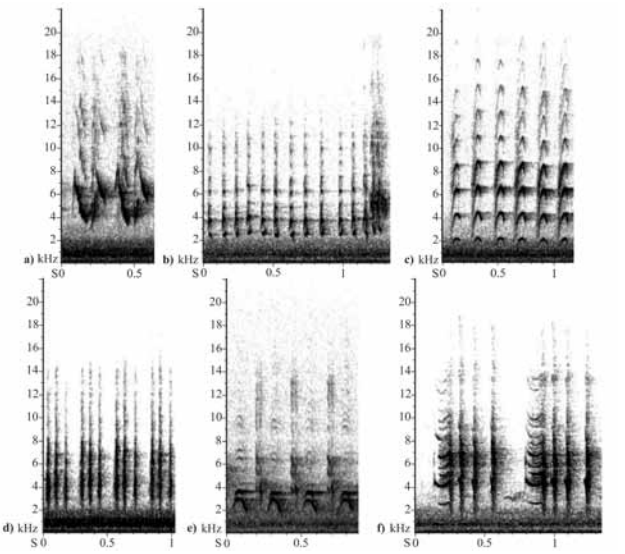

Fig. 1. *Spectrograms of six most frequently mimicked species; x scale – time(s), y scale – frequency (kHz): a)* Hirundo rustica*, b)* Turdus merula*, c)* Falco tinnunculus*, d)* Turdus pilaris*, e)* Parus major*, f)* Pica pica*.*

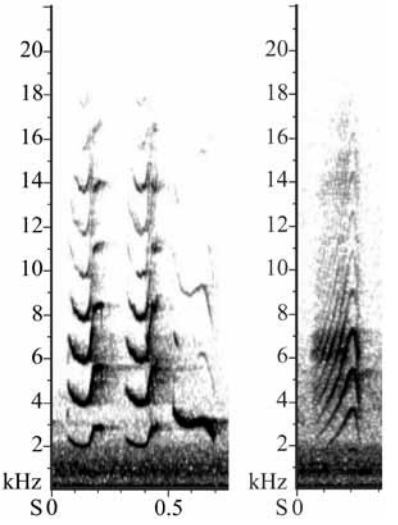

Fig. 2. *Two examples of icterine warbler specific calls; x scale – time(s), y scale – frequency (kHz).*

Table 3. *Descendent comparison of ten most frequently mimicked species by frequency and proportion of time.*

Mimicked species	% of total time	Mimicked species	Frequency [sequence/s]
Falco tinnunculus	8.3	*Hirundo rustica*	0.1186
Hirundo rustica	7.5	*Turdus merula*	0.1041
Turdus pilaris	7.3	*Falco tinnunculus*	0.0834
Turdus merula	6.7	*Turdus pilaris*	0.0495
Acrocephalus palustris	5.1	*Parus major*	0.0421
Sylvia atricapilla/borin	4.6	*Pica pica*	0.0369
Pica pica	2.8	*Passer domesticus*	0.0354
Parus major	2.7	*Acrocephalus palustris*	0.0342
Sturnus vulgaris	2.2	*Sylvia atricapilla/borin*	0.0326
Streptopelia decaocto	1.6	*Coturnix coturnix*	0.0288

visual inspection showed a high similarity. Most spectrograms of these sequences were characterized by the presence of harmonious tones (Fig. 2). From an acoustic point of view we can describe them as squeaky sounds.

Cumulative curves for each of the ten males stagnated mostly around the fifth minute and a subsequent increase after ten minutes was recorded only occasionally (Fig. 3). To cover 95 % of species mimicked a recording of 8.2 minutes is needed.

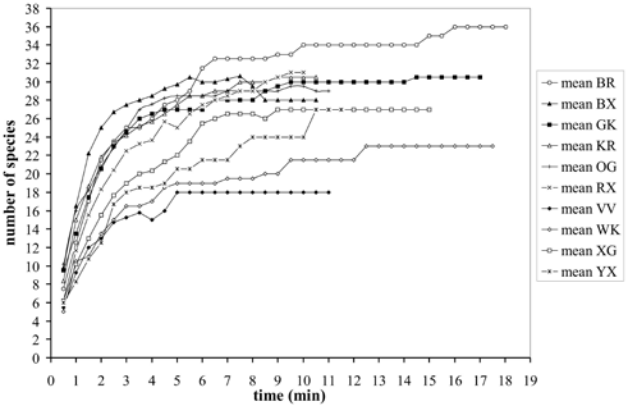

Fig. 3. *Cumulative number of mimicked species related to length of recording.*

For the PCA diagram the 18 species mimicked that best (54 %) fitted I. and II. ordination scales were chosen. The two main ordination scales accounted for 53 % of the total variation, so males demonstrated individual differences in mimetic repertoires. For example, the song of males VV and WK varied in comparison to the songs of other males that were more similar to each other (Fig. 4). This is probably caused by lower number of mimicked species in the two males (VV 15 species, WK 21 species).

Discussion

Imitations represented 76.2 % of the total time of all songs. In total, we found 42 mimicked species in the song of ten males, with a mean of 27 species per individual. The greatest proportion of species mimicked were passerines (83.3 %), the remainder was represented by five other bird orders – Accipitriformes, Galliformes, Charadriiformes, Columbiformes, Piciformes. These orders were noted in Akkermann's (2006) study too and most of the mimicked species on his species list agree with our results (69.7 %, Table 4). Two other bird orders (Ciconiiformes and Caprimulgiformes) were mentioned by Cramp (1992) and Malchevski & Pukinski (1983) but were not recorded during this study.

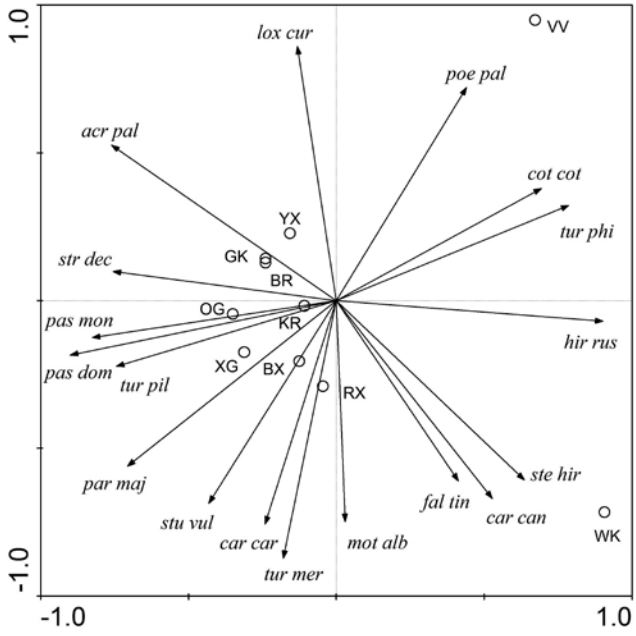

Fig. 4. *The PCA diagram for the 18 species mimicked by ten icterine warblers that best (54 %) fitted I. and II. ordination scales; two main ordination scales accounted for 53 % of the total variation; "samples" – icterine warblers: BR, BX, GK, KR, OG, RX, VV, WK, XG, YX, "species" – mimicked species, comparison based on proportion of time (% of total time); acr pal –* Acrocephalus palustris*, car car –* Carduelis carduelis*, car can –* Carduelis cannabina*, cot cot –* Coturnix coturnix*, fal tin –* Falco tinnunculus*, hir rus –* Hirundo rustica*, lox cur –* Loxia curvirostra*, mot alb –* Motacilla alba*, par maj –* Parus major*, pas dom –* Passer domesticus*, pas mon –* Passer montanus*, poe pal –* Poecile palustris*, ste hir –* Sterna hirundo*, str dec –* Streptopelia decaocto*, stu vul –* Sturnus vulgaris*, tur mer –* Turdus merula*, tur phi –* Turdus philomelos*, tur pil –* Turdus pilaris.

In total, Akkermann (2006) noted 33 species mimicked by icterine warblers. Seven other bird species were registered in a recording of a male from Sweden and another one (call of a heron *Ardea*) in a recording from Denmark (Cramp 1992) (Table 4). In a detailed study from the Leningrad region, 20 mimicked species were found in the song of icterine warblers. Some individuals imitated only three or four species, but others nine or ten. This study also found ten other mimicked species that were not recorded by Akkermann (2006) and Cramp (1992) (Table 4). The study from Sweden (Cramp 1992) mentions eight species mimicked in the song of one male within an interval of two minutes (Table 4). In contrast, our results show many more species mimicked in the same time interval (18.0 ± 4.0).

Most of the mimicked species found in the song of icterine warblers (Malchevski & Pukinski 1983,

Table 4. *Bird species noted in song of icterine warbler.*

Order	Akkermann (2006)	Cramp (1992)	Our study	Malchevski & Pukinski (1983)
Ciconiiformes	-	*Ardea sp.*	-	-
Accipitriformes	*Buteo buteo*, *Falco tinnunculus*	-	*Falco tinnunculus*	*Falco tinnunculus*
Galliformes	*Coturnix coturnix*	-	*Coturnix coturnix*	-
Charadriiformes	*Haematopus ostralegus*, *Tringa totanus*, *Vanellus vanellus*	*Sterna paradisaea*, *Vanellus vanellus*, *Numenius arquata*, *Larus canus*	*Sterna hirundo*	*Tringa ochropus, Scolopax rusticola*
Columbiformes	*Streptopelia decaocto*	-	*Streptopelia decaocto*	-
Piciformes	*Picus viridis*, *Dendrocopos major*, *Jynx torquilla*	-	*Picus viridis, Dendrocopos major*, *Jynx torquilla*	*Dendrocopos major, Dendrocopos minor*
Caprimulgiformes	-	-	-	*Caprimulgus europeus*
Passeriformes	*Alauda arvensis*, *Hirundo rustica*, *Motacilla alba*, *Acrocephalus arundinaceus, Acrocephalus scirpaceus, Sylvia atricapilla, Sylvia communis*, *Ficedula hypoleuca*, *Saxicola torquata*, *Luscinia megarhynchos, Phoenicuros ochruros*, *Turdus merula*, *Turdus pilaris*, *Turdus viscivorus*, *Parus major*, *Fringilla coelebs*, *Carduelis carduelis*, *Carduelis chloris, Carduelis cannabina, Passer domesticus, Oriolus oriolus*, *Sturnus vulgaris, Corvus monedula*	*Carpodacus erythrinus*, *Turdus viscivorus*, *Turdus philomelos*	*Alauda arvensis, Galerida cristata, Hirundo rustica, Delichon urbica, Motacilla alba, Lanius collurio, Acrocephalus palustris, Acrocephalus scirpaceus, Sylvia atricapilla/borin, Sylvia atricapilla, Phylloscopus trochilus, Phoenicurus* sp., *Erithacus rubecula, Luscinia megarhynchos, Turdus merula, Turdus philomelos, Turdus pilaris, Remiz pendulinus, Parus major, Cyanistes caeruleus, Poecile palustris, Sitta europaea, Fringilla coelebs, Carduelis carduelis, Carduelis spinus, Serinus serinus, Carduelis chloris, Loxia curvirostra, Carduelis cannabina, Coccothraustes coccothraustes, Passer domesticus, Passer montanus, Sturnus vulgaris, Garrulus glandarius, Pica pica, Corvus monedula*	*Hirundo rustica, Phylloscopus trochilus, Phoenicurus phoenicurus, Turdus pilaris, Turdus iliacus, Parus major, Fringilla coelebs, Carduelis spinus, Loxia curvirostra, Passer montanus, Oriolus oriolus, Sturnus vulgaris, Corvus monedula*
Others	calls of other African species from winter grounds		exotic species, mechanical sounds	-

Cramp 1992, Akkerman 2006, this study) are common species of urban areas. However, there are some species that occur in agricultural habitats (11.1 %); for example common buzzard (*Buteo buteo*), common quail (*Coturnix coturnix*), skylark (*Alauda arvensis*), red-backed shrike (*Lanius collurio*) and wet areas (19 %); for example northern lapwing (*Vannelus vannelus*), common redshank (*Tringa totanus*), common tern (*Sterna hirundo*), great reed warbler (*Acrocephalus arundinaceus*). In our study 81 % of species mimicked are common in urban vegetated areas. Thus, it is highly possible that there is a relationship between the acoustic environment and the song repertoire of the icterine warbler as supposed by Merciere (1921). This relationship was found for example in robin chats (*Cossypha* sp.) (Ferguson et al. 2002) and it is also one of the preconditions of learning mistakes hypothesis.

African species account for a large part (113 of 212 mimicked species) of the marsh warbler's repertoire (Dowsett-Lemaire 1979). Dowsett-Lemaire (1979) demonstrated that there is no presence of African species in the song of icterine warblers, but this is contrary to information from Akkermann (2006) and Benson (1897). We identified some potential exotic species mimicries but they made up only 0.15 % of the total time of all songs.

Imitations of mechanical sounds can often be heard in the song of the European starling (Hausberger et al. 1991) or northern mockingbird (Gander 1929). We found only one mechanical sound (gambling machine) in a recording of one male (0.05 % of total time) and therefore, we do not suppose it plays a significant role in mimicry performed by icterine warblers.

The length of recording to cover 95 % of species mimicked was estimated to be 8.2 minutes. Although graphs of only ten individuals are available, it is striking that stagnation in each of these graphs starts almost at the same time (around fifth minute) and after ten minutes there is only occasionally an increase in cumulative number. For future studies on icterine warblers, we have demonstrated here that ten minutes of recording is an appropriate amount of time to capture most of mimicked species in repertoire of an individual.

The results of PCA confirmed the existence of individual variability in species mimicked by icterine warblers, which was also noted by Cramp (1992) and Malchevski & Pukinski (1983). The causation of this variability has not been studied. We suppose that this might be connected with variation in the song models present in their habitat, which was found by Hausberger et al. (1991) for warbling part of European starlings' song. One of the topics we are investigating further is the cause of mimicry variation in this icterine warbler population.

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