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INDIVIDUAL INFORMATION AND NEIGHBOUR-STRANGER DISCRIMINATION IN A SUBOSCINE LEKKING SPECIES: THE SCREAMING PIHA (*Lipaugus vociferans*)

ABSTRACT

Because suboscine innate songs are generally less variable than those culturally acquired in their sister taxa, the oscine passerines, they are thought to convey less information. However, in this group, acoustic individual variations have been found in several species, with heterogeneous faculties of recognition. The Screaming Piha is a neotropical lekking suboscine, whose famous trisyllabic song have been shown to bear an individual signature. To corroborate this assertion, we investigated vocal variations of 8 recorded males from 3 leks, by conducting fine structural analysis on their spectrograms. We found that the main syllables of the song had sufficient interindividual variability to predict accurately the identity of the singer, mainly based on their highest frequencies. Moreover, neighbour-stranger playback experiments conducted on 12 individuals within 4 leks revealed that they could discriminate between familiar and unfamiliar songs. Tested birds continued displaying after hearing their neighbour's vocalizations, whereas they significantly reduced their song rate or stopped singing in response to unknown ones. Those results confirm the existence of an individual vocal distinctiveness in the Screaming Piha, relying on acoustic features which are likely to be transmitted to a private audience, and demonstrate its ability to recognize it. We discuss the biological meaning of the responses obtained, and suggest further investigations.

Introduction

Songs, in birds, are particular signals emitted spontaneously with two main functions: attracting potential mates and repelling intrasexual rivals [1]. Thus, they convey a huge amount of singer-related information, such as species [2], sex [3], social status [4], physical condition [5, 6, 7], age [4, 8, 9], body mass [10], hormonal levels [7] or immediate motivation and aggressiveness [11, 12, 13]. Above all, signaling individual identity is necessary in many social functions such as mate [14, 15] and parent-offspring recognition [16, 17] or territorial defense [18,19]. Because these characteristics are encoded by structural and syntactic variations, they are widely studied in songbirds, which often express a highly complex vocal repertoire, acquired through vocal learning [20]. However, the way simpler and even stereotyped songs are able to communicate such information remains incompletely understood, especially when it comes to their sister taxa, the suboscines, whose vocalizations are innate [21, 22, 23]. In this group, an individual vocal signature, or in other words, an intra-individual song variation in one or several parameters smaller than the interindividual variation, has been found in several species: the Eastern Wood-Pewee (*Contopus virens*) [24], the Buff-breasted Flycatcher *(Empidonax fulvifrons)* [25], the Southwestern Willow Flycatcher (*Empidonax traillii extimus)* [26], the Mexican Ant-thrushe (*Formicarius moniliger*) [27], the Eastern Phoebe (*Sayornis Phoebe*) [28] and the Screaming Piha (*Lipaugus vociferans*) [29]. Nevertheless, if such acoustic features are a necessary condition to achieve individual identification based on songs, playback experimental designs have to be set up to confirm their biological relevance. The Alder flycatcher (*Empidonax alnorum*), for instance, has been shown to have the ability to discriminate between songs of neighbours and strangers, and responded more aggressively to broadcasted unfamiliar songs [30], whereas in two other species, the Acadian flycatcher (*Empidonax virescens*) and the spotted antbird (*Hylophylax naevioides*) [31, 32], no significant difference have been found.

Here we focus on the Screaming Piha, a neotropical Cotingidea, whose stereotyped trisyllabic song, reaching 111,5 dB at 1 meter [33], is emblematic of the Amazonian forest soundscape. Each vocalization consist in an introductory sequence with paired low frequency-modulated and low amplitude syllables (roo-roo), followed by two explosive high frequency-modulated syllables ("pee-haw"). In some contexts which remain unclear, series of "we-oo" calls can also be heard [34]. Because it lives under the canopy, at about 50 meters from his neighbours [34], with very little visual cues, its social interactions mostly rely on acoustic communication. Indeed, in this suboscine species, males gather year-around in exploded leks, where they display during the whole day [35], moving from branch to branch within their territory. Those social structures are highly competitive polygynous systems [36, 37] in which males have unequal reproductive success, generally depending on their relative position from the center of the lek [38, 39, 40]. As constant territorial defence is energetically costly, we think that the Screaming Piha could have the faculty to discriminate his direct neighbour's song from stranger songs, especially as leks composition appear usually stable [41, 42, 43, 44]. In this species, allegations about the existence of an individual vocal signature [29, 45] suffered from several methodological bias [46]. To test our hypothesis, we first try to confirm those previous results and to identify the acoustical features involved, before to conduct playback experiments. We expect to observe a more aggressive response towards unknown songs than to familiar songs, i.e. a "dear enemy" effect [47].

Materials and methods

Song structure analysis

8 individuals from 3 leks were recorded 9 to 14 times in different areas in French Guiana, on a one-week period in 2008. Recording sessions were conducted on several days and different contexts for each individual, using a long gun microphone Sennheiser MKH 70-1, and two different recorders, Marantz and Nagra, with a 48 kHz sampling frequency. To minimize signal deterioration, each bird was recorded just below its tree perch. Because individuals were not banded, they were identified by their GPS coordinates and their relative position in the lek. Indeed, it has been assumed that as in many species, lek composition and territory occupancy were likely to be stable, especially on such a reduced period. In each recording, a unique good quality vocalization has been selected for further analysis. Because introductory syllables were not always correctly defined on the spectrogram, manual measurements were only conducted on main syllables "pee-haw", as described in Figure.1. All spectrogram analysis were handled using Praat software. The 16 frequency values obtained were kept as variables. New acoustical parameters were also calculated: 4 durations, 9 frequency modulations, 4 bandwidths and 6 parameters assessing the relative position of major amplitude points in their respective syllable (cf Table 1). Those 39 variables were used in the following statistical analysis.

A multivariate analysis was first conducted to test the existence of an individual signature in the Screaming Piha's song. In order to reduce redundancy among acoustical parameters, a principal component analysis was performed, and only the first 8 components (explaining 87,53% of the variability among vocalizations) with higher-than-one eigenvalues were selected and used as new variables in a canonical discriminant analysis. Then, a posterior confusion matrix was obtained by cross-validation, using equal prior probabilities for each individual.

In an attempt to characterize the song features involved in vocal identity, we performed a univariate non parametric Kruskall-Wallis test to identify the most variable acoustical parameters among recorded birds. Results where compared to the 8 components' canonical weights: the loadings of those presenting higher coefficients were then examined to find highly correlated acoustical parameters -and thus highly discriminant signal parts-. The multivariate analysis described previously was finally performed again, on a reduced number of selected variables.
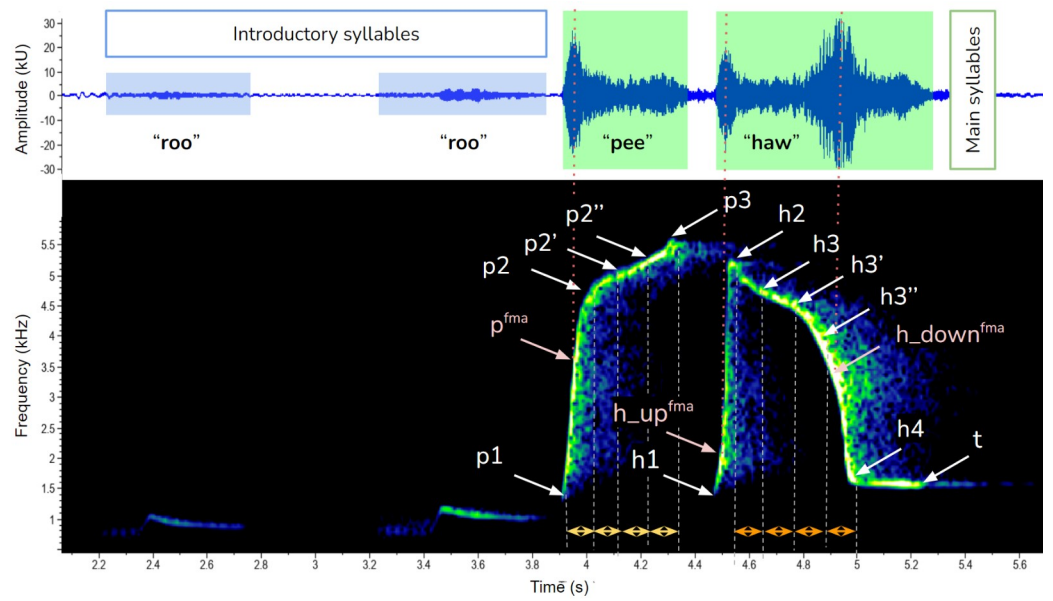
Figure 1: Oscillogram and corresponding spectrogram of a stereotyped trisyllabic song. Time and frequency values were measured on 16 points defined on the spectrogram: p1, p3 = minimal and maximal frequency of the « pee » syllable ; p2, p2', p2''= frequencies at respectively ¼,½,¾ of the « pee » syllable length ; h1, h2 =minimal and maximal frequency of the « haw » syllable ascending part; h4=minimal frequency of the « haw » syllable ascending part ; h3, h3', h3''= frequencies at respectively ¼,½,¾ of the « haw» syllable descending part length ; t= terminal frequency ; p^{fma}, h_up^{fma}, h_down^{fma} = frequency of major amplitude within the « pee » syllable and « haw » syllable ascending and descending parts.

Table 1, Calculated variables (durations, frequency modulations, bandwidths, FMA's relative position) using the 16 time and frequency values measured as showed on Figure 1.

|	Variable	Formula
Duration	a	$p3(t) - p1(t)$
	b1	$h2(t) - h1(t)$
	b2	$h4(t) - h2(t)$
	b3	$t(t) - h4(t)$
Frequency modulations	s1_pee	$[p2(f) - p1(f)] / [p2(t) - p1(t)]$
	s2_pee	$[p2'(f) - p2(f)] / [p2'(t) - p2(t)]$
	s3_pee	$[p2''(f) - p2'(f)] / [p2''(t) - p2'(t)]$
	s4_pee	$[p3(f) - p2''(f)] / [p3(t) - p2''(t)]$
	s_haw_up	$[h2(f) - h1(f)] / [h2(t) - h1(t)]$
	s1_haw_down	$[h3(f) - h2(f)] / [h3(t) - h2(t)]$
	s2_haw_down	$[h3'(f) - h3(f)] / [h3'(t) - h3(t)]$
	s3_haw_down	$[h3''(f) - h3'(f)] / [h3''(t) - h3'(t)]$
	s4_haw_down	$[h4(f) - h3''(f)] / [h4(t) - h3''(t)]$
Bandwidth	BW_pee	$p3(f) - p1(f)$
	BW_haw_up	$h2(f) - h1(f)$
	BW_haw_down	$h2(f) - h4(f)$
	BW_tail	$h4(f) - t(f)$
FMA's relative position	FMA_pee_FREQ	$[p^{fma}(f) - p1(f)] / BW\_pee$
	FMA_pee_TIME	$[p^{fma}(t) - p1(t)] / a$
	FMA_haw_up_FREQ	$[haw\_up^{fma}(f) - h1(f)] / BW\_haw\_up$
	FMA_haw_up_TIME	$[haw\_up^{fma} - h1(t)] / b1$
	FMA_haw_down_FREQ	$[haw\_down^{fma}(f) - h2(f)] / BW\_haw\_down$
	FMA_haw_down_TIME	$[haw\_down^{fma}(t) - h2(t)] / b2$
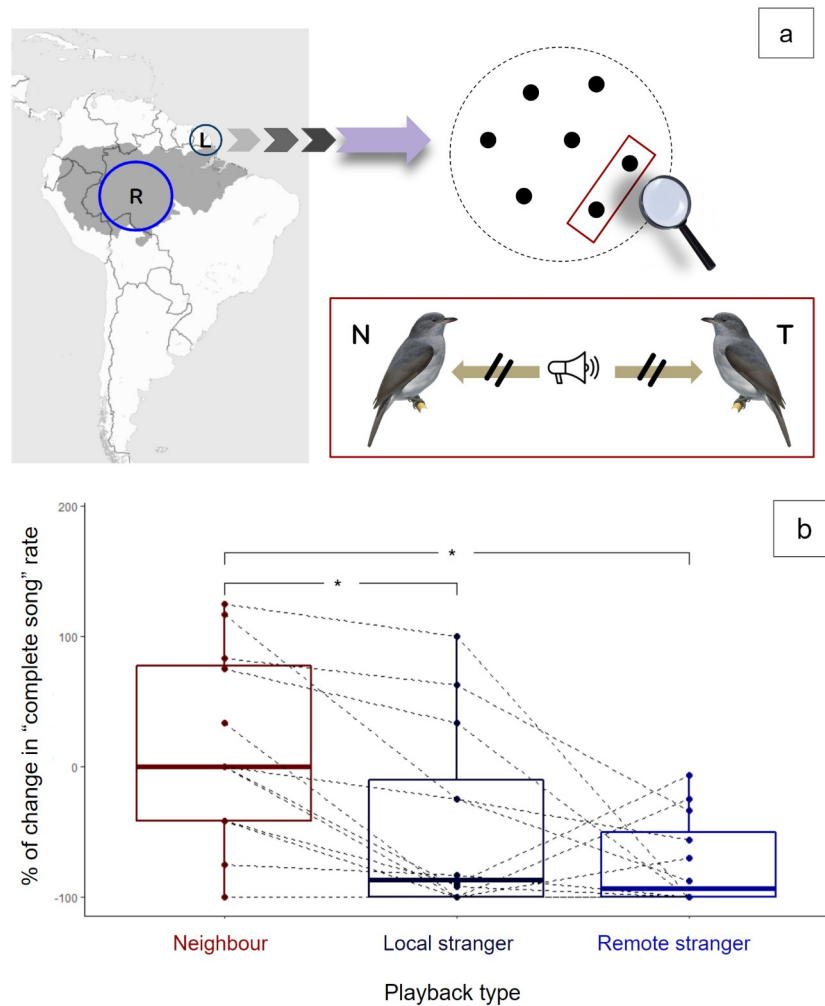
Figure 2. Playback test design and results a) The map specifies the origin of the vocalizations used in the playback tracks: "R" = "Remote stranger" and "L"= "Local stranger". On the right: schematic representation of a Guyanese lek and the distribution of its members (black dots). The red box corresponds to a couple of selected individuals: "N"="Neighbour", whose song was broadcasted to "T"=Tested individual, by an equidistant loudspeaker set up towards the latter, to mimic the presence of a bird at its territory borders (without crossing it). b) Percentage of change in "complete song" (at least one introductory syllable followed by "pee-haw" syllables) rate before and after each playback type. A significant decrease is noted as a response to both stranger playback types compared to neighbour's broadcasted songs.

Playback experiments

All playback experiments were carried out in French Guiana, on a two-week period in November 2021, within 4 leks: 2 were located near the Nouragues research station (Lek 3 and 4), and 2 others in Roura area (Lek 1 and 2).

12 individuals were each tested with three types of playback. The first one, called "Neighbour", consisted of songs recorded from an individual occupying a territory bordering on theirs. The others correspond to songs unknown to the tested bird, one composed of vocalizations of distant Guyanese conspecifics ("Local stranger"), and the other of songs of individuals from the southern Amazon basin ("Remote stranger"). They came in part from the online database xeno-canto.org and some songs recorded in leks 1 and 2 were also used as Guyanese signals for tests in leks 3 and 4. All recordings were made using a long gun microphone Sennheiser MKH 70-1 and 3 different recorders: Zoom H4n Pro, Marantz and Nagra. In order to limit background noise, each vocalization has been manually filtered with Avisoft-SASLab Pro and the peak

amplitude has been normalized. In order to avoid pseudo-replication, each playback track has been used only once (in total 36 were used, 12 for each playback type).

Using GPS coordinates, a Foxpro Fusion speaker was attached to a tree branch at about 5 meters high, equidistant from the tested individual and his neighbour. When both of them were displaying, the tested bird was recorded during 1 minute, before broadcasting the playback. The same trisyllabic vocalization was repeated 3 times interspersed with 10 seconds of silence -matching with the mean frequency observed in natural displays-, with an average sound level of 90 dB at one meter. Since then, the vocal and behavioural response were monitored during 2 minutes, recorded and commented by two blind observers. Other trials were conducted only when the tested individuals and his neighbour had returned to their prestimulus singing rates, and we waited at least 15 minutes when they remained unchanged during the experiment. To minimize rank effect, playback types were broadcasted in equally distributed orders among tested individuals. Furthermore, to avoid problems such as habituation to the speaker, nearby individuals were not tested on the same day.

Two variables were finally calculated : the number of calls (« wee-oo ») within the response, and the percentage of change in « complete song » rate before and after the playback. A score, from -1 to 2, was also assigned to describe the tested bird's movements. 0 was given when it remained immobile, and -1 when it moved back. Approached movements were graded 1 or 2 depending on their amplitude. 2 was given if the individuals almost reached or flew over the loudspeaker, and 1 if it was more discrete. Tested birds remained most of the time invisible, and behavioural observations relied mostly on subjective localization of their songs by the observers, which were later confirmed by amplitude comparisons on the spectrograms.

Non-parametric sample-paired statistical tests were used to assess the impact of each playback: a Friedman test and a post-hoc Wilcoxon test were applied to each of the three variables.

Results

Song structure analysis

The canonical discriminant analysis predicted 84,71 % of the 85 vocalizations to the correct individual, way above the 16,47 % of accurate classification at chance level (CI = [0.7527, 0,916], p-value=<2.2e-16, Kappa= 0.8247), even if misclassifications were noticed between two birds whose song structure appeared to be very similar on the spectrograms.

Kruskall-Wallis tests revealed differences among individuals for each acoustical variable, but with heterogeneous significance levels. Most discriminant variables are reported in table 2.

Table 2*: 8 most significant variables at Kruskall-Wallis tests, with 7 degrees of freedom.*

Variable	Kruskall-Wallis X^2	p-value
p3(f)	76.761	6.29e-14
p2''(f)	76.105	8.551e-14
p'2(f)	74.62	1.713e-13
h2(f)	73.62	2.733e-13
b2	71.85	6.242e-13
BW_haw_down	71.277	8.151e-13
BW_pee	68.099	3.574e-12
p2(f)	67.052	5.812e-12

A confusion matrix, based on the 4 most discriminant frequencies, p3 (f), p2''(f), p'2(f) and h2 (f), show that they are sufficient to predict individual's identity (Accuracy = 0.6941, 95% CI: (0.5847, 0.7895), No Information Rate = 0.1647, p-value < 2.2e-16, Kappa = 0.6514).

Playback experiments

Friedman test (n=12) revealed no significant difference between «Remote stranger», «Local stranger» and «Neighbour» playback-type responses, in terms of movements (X^2=2,74 p-value=0,254) and number of calls (X^2=2,95 p-value=0,229). However, few birds emitted calls but almost all of them were heard after stranger-song playbacks. 2 birds called in response to remote stranger vocalizations, 4 in response to local stranger songs, and only one individual replied with a unique call to his neighbour's song. In contrast, clear variations in percentage of change of « complete song » rate were found (X^2=14,37 p-value=0,00076), and Wilcoxon test showed a significant decrease in response to both stranger playbacks (with mean percentage = -43,26 % and -73,19 % ; p-values=0,012 and 0,034 for respectively «Local stranger » and « Remote stranger » types) compared to "Neighbour" songs (mean percentage=14,58%). In response to familiar songs, half of the individuals enhanced their songs rate, whereas others slightly reduced it (median= 0%).

Discussion

Our analysis confirmed in part the results published in Fitzsimmons et al. 2008 [29], in which songs were predicted to the correct individual with a 93,2% accuracy after a canonical discriminant analysis, but most criticisms formulated against it [46] were avoided here. Nevertheless, misclassifications we observed between vocalizations of two particular recorded birds could show the limits of GPS identification, as those non-banded individuals are likely to be the same. We also have not been able to assess the amount of individual information encoded in introductory syllables, often emitted independently: it had previously been showed as low, but significant. Modulation frequency amplitudes of both main syllables had also been pointed out to be the most interindividually variable parameters, and our results support and complete this claim by showing that those bandwidths are modulated in major part by the highest frequencies. Indeed, maximum frequencies among our 8 individuals ranged from 5018 Hz to 5554 Hz for the "pee" syllable and from 4235 to 4826 Hz for the "haw" syllable. On the contrary, the "haw" syllable ascending part duration didn't play a significant discriminant role in our analysis, but its descending portion is likely to be involved. In dense forests, high frequency signals tend to be more sensible to degradation and are often transmitted on restricted distances [48, 49]. Thus, the individual signature is bound to be a "private" information [50] transmitted to a reduced audience, limited to their direct neighbours in the lek. In the white-browed warbler (*Basileuterus leucoblepharus*) for instance, individual acoustic features, contained between 5 and 7 kHz, do not propagate over 100 m [51]. In the Screaming Piha however, this phenomenon could be counter-balanced by the loudness of its songs, even if major amplitude frequencies values are generally mostly around 3-4 kHz. Propagation experiments are therefore required to test this hypothesis.

Playback results showed significant differences between responses to neighbour and stranger songs, highlighting hence the ability of song-based individual discrimination in this species. Whether we can conclude to the existence of a "dear enemy" effect or not remains however ambiguous, as, unlike territorial birds, they became mostly quite when unknown songs were broadcasted, while they continued singing after hearing familiar vocalizations. As a consequence, counter-songs might not be reliable indicators of hostility in this lekking species, and may on the contrary be considered as an increase of motivation to go on displaying. Leks, indeed, far from being barely competitive structures, are also mutual benefit social systems in which males pool their energy to attract females [37, 52]. Besides, surprise or aggressivity could be expressed by calls often coupled with approaches, which were difficult to monitor on silent individuals and thus certainly underestimated. Similar results were obtained in another suboscine species, the ochre-bellied Flycatcher

(*Mionectes oleagineus*) [53], in which lekking individuals responded to stranger playbacks by reducing their song rate and moving to the loudspeaker.   In any case, individuals detected accurately irregular songs and future perspectives should be to test if those discrimination abilities can be extended to individual neighbour recognition, demonstrated in a unique suboscine species, the Alder flycatcher (*Empidonax alnorum*) [54].

Bibliography

[1] CATCHPOLE, C. K. et SLATER, P. J. B. Bird Song: Biological Themes and Variations. Cambridge Univ Press. Cambridge, UK, 2008.

[2] BECKER, Peter H. The coding of species-specific characteristics in bird sounds. In : Acoustic communication in birds. academic press, 1982. p. 213-252

[3] HOELZEL, A. RUS. Song characteristics and response to playback of male and female robins Erithacus rubecula. Ibis, 1986, vol. 128, no 1, p. 115-127.

[4] BOTERO, Carlos A., ROSSMAN, Rachel J., CARO, Lina M., *et al.* Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, 2009, vol. 77, no 3, p. 701-706.

[5] SPENCER, Karen A., BUCHANAN, Katherine L., LEITNER, Stefan, et al. Parasites affect song complexity and neural development in a songbird. Proceedings of the Royal Society B: Biological Sciences, 2005, vol. 272, no 1576, p. 2037-2043.

[6] BUCHANAN, Katherine L., CATCHPOLE, C. K., LEWIS, J. W., et al. Song as an indicator of parasitism in the sedge warbler. Animal behaviour, 1999, vol. 57, no 2, p. 307-314.

[7] GALEOTTI, PAOLO, SAINO, Nicola, SACCHI, ROBERTO, et al. Song correlates with social context, testosterone and body condition in male barn swallows. Animal behaviour, 1997, vol. 53, no 4, p. 687-700.

[8] GALEOTTI, Paolo, SAINO, Nicola, PERANI, Elena, et al. Age-related song variation in male barn swallows. Italian Journal of Zoology, 2001, vol. 68, no 4, p. 305-310.

[9] GIL, Diego, COBB, James LS, et SLATER, Peter JB. Song characteristics are age dependent in the willow warbler, Phylloscopus trochilus. Animal Behaviour, 2001, vol. 62, no 4, p. 689-694.

[10] BERTELLI, Sara et TUBARO, Pablo L. Body mass and habitat correlates of song structure in a primitive group of birds. *biological Journal of the Linnean Society*, 2002, vol. 77, no 4, p. 423-430.

[11] SEARCY, William A. et BEECHER, Michael D. Song as an aggressive signal in songbirds. Animal Behaviour, 2009, vol. 78, no 6, p. 1281-1292.

[12] AKÇAY, Çağlar, ANDERSON, Rindy C., NOWICKI, Stephen, et al. Quiet threats: soft song as an aggressive signal in birds. Animal Behaviour, 2015, vol. 105, p. 267-274.

[13] BEECHER, Michael D. et CAMPBELL, S. Elizabeth. The role of unshared songs in singing interactions between neighbouring song sparrows. Animal Behaviour, 2005, vol. 70, no 6, p. 1297-1304.

[14] SPEIRS, Elizabeth AH et DAVIS, Lloyd S. Discrimination by Adélie Penguins, Pygoscelis adeliae, between the loud mutual calls of mates, neighbours and strangers. *Animal Behaviour*, 1991, vol. 41, no 6, p. 937-944.

[15] ROBERTSON, Bruce C. Vocal mate recognition in a monogamous, flock-forming bird, the silvereye, Zosterops lateralis. *Animal behaviour*, 1996, vol. 51, no 2, p. 303-311.

[16] AUBIN, Thierry et JOUVENTIN, Pierre. Cocktail–party effect in king penguin colonies. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 1998, vol. 265, no 1406, p. 1665-1673.

[17] CHARRIER, Isabelle, MATHEVON, Nicolas, et JOUVENTIN, Pierre. Mother's voice recognition by seal pups. *Nature*, 2001, vol. 412, no 6850, p. 873-873.

[18] BRIEFER, Elodie, RYBAK, Fanny, et AUBIN, Thierry. When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, Alauda arvensis. *Animal Behaviour*, 2008, vol. 76, no 4, p. 1319-1325.

[19] STODDARD, Philip Kraft. 20. Vocal Recognition of Neighbors by Territorial Passerines. In : *Ecology and evolution of acoustic communication in birds*. Cornell University Press, 2019. p. 356-374.

[20] KROODSMA, Donald E. et MILLER, Edward H. (ed.). *Ecology and evolution of acoustic communication in birds*. Comstock Pub., 1996.

[21] TOUCHTON, Janeene M., SEDDON, Nathalie, et TOBIAS, Joseph A. Captive rearing experiments confirm song development without learning in a tracheophone suboscine bird. PloS one, 2014, vol. 9, no 4, p. e95746.

[22] KROODSMA, Donald E. Songs of the Alder Flycatcher (Empidonax alnorum) and Willow Flycatcher (Empidonax traillii) are innate. The Auk, 1984, vol. 101, no 1, p. 13-24.

[23] KROODSMA, Donald E. et KONISHI, Masakazu. A suboscine bird (eastern phoebe, Sayornis phoebe) develops normal song without auditory feedback. Animal Behaviour, 1991, vol. 42, no 3, p. 477-487.

[24] CLARK, J. Alan et LEUNG, Justina. Vocal distinctiveness and information coding in a suboscine with multiple song types: Eastern Wood-Pewee. The Wilson Journal of Ornithology, 2011, vol. 123, no 4, p. 835-840. 115

[25] LEIN, M. Ross. Song variation in Buff-breasted Flycatchers (Empidonax fulvifrons). The Wilson Journal of Ornithology, 2008, vol. 120, no 2, p. 256-267.

[26] FERNÁNDEZ-JURICIC, Estrban, DEL NEVO, Aadrian J., et POSTON, Rachael. Identification of individual and population-level variation in vocalizations of the endangered Southwestern Willow Flycatcher (Empidonax traillii extimus). The Auk, 2009, vol. 126, no 1, p. 89-99.

[27] KIRSCHEL, Alexander NG, CODY, Martin L., HARLOW, Zachary T., et al. Territorial dynamics of Mexican Ant-thrushes Formicarius moniliger revealed by individual recognition of their songs. Ibis, 2011, vol. 153, no 2, p. 255-268.

[28] FOOTE, Jennifer R., PALAZZI, Erica, et MENNILL, Daniel J. Songs of the Eastern Phoebe, a suboscine songbird, are individually distinctive but do not vary geographically. Bioacoustics, 2013, vol. 22, no 2, p. 137-151.

[29] FITZSIMMONS, Lauren P., BARKER, Nicole K., et MENNILL, Daniel J. Individual variation and lek-based vocal distinctiveness in songs of the Screaming Piha (Lipaugus vociferans), a suboscine songbird. The Auk, 2008, vol. 125, no 4, p. 908-914.

[30] LOVELL, Scott F. et LEIN, M. Ross. Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, Empidonax alnorum. *Behavioral Ecology*, 2004, vol. 15, no 5, p. 799-804.

[31] WILEY, R. Haven. Individuality in songs of Acadian flycatchers and recognition of neighbours. Animal Behaviour, 2005, vol. 70, no 1, p. 237-247.

[32] BARD, Susanne C., HAU, Michaela, WIKELSKI, Martin, et al. Vocal distinctiveness and response to conspecific playback in the spotted antbird, a Neotropical suboscine. The Condor, 2002, vol. 104, no 2, p. 387-394.

[33] NEMETH, ERWIN. Measuring the sound pressure level of the song of the Screaming Piha Lipaugus vociferans: One of the loudest birds in the world?. Bioacoustics, 2004, vol. 14, no 3, p. 225-228.

[34] SNOW, Barbara K. Notes on the behavior of three Cotingidae. The Auk, 1961, vol. 78, no 2, p. 150-161.

[35] ULLOA, Juan Sebastian, GASC, Amandine, GAUCHER, Phillipe, et al. Screening large audio datasets to determine the time and space distribution of Screaming Piha birds in a tropical forest. Ecological informatics, 2016, vol. 31, p. 91-99.

[36] BRADBURY, J. W. The evolution of leks. Natural selection and social behavior, 1981, p. 138-169.

[37] WILEY, R. Haven. Lekking in birds and mammals: behavioral and evolutionary issues. Advances in the Study of Behavior, 1991, vol. 20, p. 201-291.

[38] HÖGLUND, Jacob et LUNDBERG, Arne. Sexual selection in a monomorphic lek-breeding bird: correlates of male mating success in the great snipe Gallinago media. Behavioral Ecology and Sociobiology, 1987, vol. 21, no 4, p. 211-216.

[39] RINTAMÄKI, Pekka T., HÖGLUND, Jacob, ALATALO, Rauno V., et al. Correlates of male mating success on black grouse (Tetrao tetrix L.) leks. In : Annales Zoologici Fennici. Finnish Zoological and Botanical Publishing Board, 2001. p. 99-109.

[40] FISKE, Peder, RINTAMÄKI, Pekka T., et KARVONEN, Eevi. Mating success in lekking males: a meta-analysis. Behavioral Ecology, 1998, vol. 9, no 4, p. 328-338.

[41] HÖGLUND, Jacob et ALATALO, Rauno V. Leks. Princeton University Press, 2014.

[42] STILES, F. Gary et WOLF, Larry L. Ecology and evolution of lek mating behavior in the long-tailed hermit hummingbird. Ornithological monographs, 1979, no 27, p. iii-78.

[43] LILL, Alan. Lek behavior in the golden-headed manakin, Pipra erythrocephala in Trinidad (West Indies). Fortschritte der Verhaltensforschung, 1976.

[44] HOVI, Matti, ALATALO, Rauno V., et RINTAMÄKI, Pekka T. Habitat differences and variability in the lek mating system of black grouse. Behaviour, 1996, p. 561-578.

[45] FITZSIMMONS, Lauren P., BARKER, Nicole K., et MENNILL, Daniel J. Further analysis supports the conclusion that the songs of Screaming Pihas are individually distinctive and bear a lek signature. The Auk, 2011, vol. 128, no 4, p. 790-792.

[46] KROODSMA, Donald. Neither individually distinctive songs nor "lek signatures" are demonstrated in suboscine Screaming Pihas. The Auk, 2011, vol. 128, no 4, p. 789-790.

[47] TUMULTY, James P., VONK, J., et SHACKELFORD, T. Dear enemy effect. Encyclopedia of Animal Cognition and Behavior. Springer International Publishing, Cham, Switzerland, 2018, p. 1-4

[48] MORTON, Eugene S. Ecological sources of selection on avian sounds. *The American Naturalist*, 1975, vol. 109, no 965, p. 17-34.

[49] MATHEVON, Nicolas, AUBIN, Thierry, et BRÉMOND, Jean-Claude. Propagation of bird acoustic signals: comparative study of starling and blackbird distress calls. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*, 1997, vol. 320, no 11, p. 869-876.

[50] MCGREGOR, Peter K. (ed.). Animal communication networks. Cambridge University Press, 2005

[51] MATHEVON, Nicolas, AUBIN, Thierry,s VIELLIARD, Jacques, et al. Singing in the rain forest: how a tropical bird song transfers information. PLoS One, 2008, vol. 3, no 2, p. e1580.

[52] ALATALO, Rauno V., HÖGLUND, Jacob, LUNDBERG, Arne, et al. Evolution of black grouse leks: female preferences benefit males in larger leks. Behavioral Ecology, 1992, vol. 3, no 1, p. 53-59.

[53] WESTCOTT, David A. Neighbours, strangers and male-male aggression as a determinant of lek size. Behavioral Ecology and Sociobiology, 1997, vol. 40, no 4, p. 235-242.

[54] LOVELL, Scott F. et LEIN, M. Ross. Individual recognition of neighbors by song in a suboscine bird, the alder flycatcher Empidonax alnorum. *Behavioral Ecology and Sociobiology*, 2005, vol. 57, no 6, p. 623-630.