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ARTICLE

Flight-call as species-specific signal in South American parrots and the effect of species relatedness in call similarity

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ABSTRACT: Vocal communication is fundamental to regulate the social interactions in most gregarious species especially after dispersal movements for foraging or predator escape. A species common acoustic signal may be beneficial to group members and is especially critical in species that disperse large distances like parrots. In this study, we investigated whether parrots flight-calls carry species-specific characteristics and tested its variability within and across species. We also assessed the hypothesis of relationship between similarity in species flight-calls and phylogeny. We studied the flight-calls of 10 parrot species all occurring in Cerrado habitat in central Brazil. Our results show that, spectrum wise, there is not a discrete spectral partition between species flight-calls. Flight-calls are conservative within most of the species. Both spectral and temporal dimensions contribute to the difference between species. The species specificity of the calls was confirmed by cross correlation approach. Nevertheless, we found a difference in the call variability with some species exhibiting stereotyped calls (*e.g. Amazona aestiva*) while others exhibited variable calls (*Brotogeris chiriri*), suggesting that the function of the flight-call may differ between species, from conveying species signatures to more specific information like group or individual signature. As expected, closely related species have more similar calls. These results show that parrots flight-calls have species-specific characteristics. In some species, these calls can potentially be used in the maintenance of the group or could code other type of information, suggesting that flight-calls may play different roles depending of the species life history.

KEY-WORDS: animal communication, bioacoustics, Cerrado, Neotropical, Psittacidae, species signature.

INTRODUCTION

Species-specific acoustic signals are largely found in animal species including different taxa as fishes, frogs, birds and mammals (Obrist *et al.* 2010). These signals, usually calls or songs, are best known in situations of territorial defence or mate attraction. Species-specific acoustic signals play an important role in the species survival and reproduction, and are key to the mechanisms of reproductive isolation (Bradbury & Vehrenkamp 1998), preventing species misidentifications while allowing for proper mate choice. However, other types of vocalizations used in contexts such as social behaviour may also contain species-specific information, and could be important to understanding the evolution of species-specifics signals.

Social behaviour is widely found and communication can be important to regulate group activities such as in the maintenance of group cohesion and searching for resources. Species-specific signal (or group- or population-specific signal) enables individuals to recognize each other as belonging to the same species or to specific groups that can be organized from the species level, but also in smaller roosting, foraging or family groups.

Flight-calls occur in a considerable number of species usually associated with gregarious habits like flock foraging, nocturnal group migration or roosting (Kleeman & Gilardi 2005, Farnsworth & Lovette 2008). Few studies addressed flight-calls as species-specific signals, even thought stereotyped flight-calls have enough encoded information to allow for monitoring nocturnal migration through call classification by qualified personnel (Graber & Cochran 1960, Hüppop & Hilgerloh 2012). However, information about non-migratory flight-calls is limited and in some cases it was found to be less stereotyped varying substantially between individuals, populations, and across species distribution range (Wright 1996, Wanker *et al.* 1998, Baker 2000, Kleeman & Gilardi 2005, Wanker *et al.* 2005, Berg *et al.* 2011).

Flight-calls characteristics depends of several factors from species size, which constrains frequency usage (Torres *et al.* 2017), to habitat, which can potentially mould call structure and frequency (Chapuis 1971, Morton 1975), resulting in convergence in duration, frequency or amplitude (Farnsworth & Lovette 2008). The acoustic environment constrains the evolution of flight-call especially in species that occur in complex acoustic environments both from other animals and from the abiotic elements (Chapuis 1971, Morton 1975, Ryan & Brenowitz 1985). Additionally, the presence of acoustic competing species could favour the evolution of signals with little mutual interference, promoting vocal divergence by the spectral partition of the acoustical space (Seddon 2005). On the other hand, flight-call differentiation between species should be to some extent constrained by species relatedness, and could still retain phylogenetic information (Ryan & Brenowitz 1985, Vielliard 1995, 1997). Contrary to signals involved in mate acquisition process (*e.g.* functioning as a reproductive isolation mechanism like songs), there is little information on the selective pressures driving the evolution of flight-calls, or if close-related species in fact present similar call characteristics.

Here we investigate flight-calls as possible species-specific signals using a comparative approach. We examined flight-calls from 10 parrot species occurring in the Cerrado (central Brazil), which holds a diverse parrot community. Neotropical parrots are vocally active species that usually form small foraging groups during the day, and yet roost in large numbers during the night (Rasmussen 1999). Because of the dependence upon long range-communication, parrots are a great group to investigate flight-calls in the light of species-specific information. Initially, we compared flight-call dominant frequencies to investigate whether they are spectrally partitioned. We were expecting that species exhibited vocalizations spectrally segregated in order to avoid acoustical interference. We assessed between species flight-call variation to examine the segregation in the acoustical space, and used call parameters to classify the calls among species through a multinomial regression approach. We also examined the similarity of the calls, specifically to test if the similarities within species were higher than the similarities between species, as expected in a species-specific signal. Finally, we build a dendrogram based on the acoustical parameters, and compared it to the topology of published phylogenies.

METHODS

Species and study area

The Cerrado is the second largest Neotropical biome and is a unique savannah biodiversity hotspot (Myers *et al.* 2000, Mittermeier *et al.* 2005). Cerrado holds populations of 33 parrot species (Silva 1995), representing almost 40% of all Brazilian parrot species (Piacentini *et al.* 2015). Here we used the most common species, recorded by us within the heart of Cerrado along the state of Goiás and Federal District (Brazil). We analyzed flight-calls of the following species: *Amazona aestiva* (Aae), *Alipiopsitta xanthops* (Axa), *Ara ararauna* (Aar), *Eupsittula aurea* (Eau), *Psittacara leucophthalma* (Ple), *Brotogeris chiriri* (Bch), *Diopsittaca nobilis* (Dno), *Forpus xanthopterygius* (Fxa), *Orthopsittaca manilata* (Oma) and *Pionus maximiliani* (Pma).

Sound recordings

Flight-calls were recorded using a Sony PCM-D50 digital recorder (Sony Electronics Inc., Japan), coupled with a parabola dish (50 cm diameter and 19 cm of focus) and a Shure Beta58a microphone (Shure Inc., USA). The recordings were made on Emas National Park (GO), São Manuel farm (Formosa, GO), Nossa Senhora Aparecida Farm (Monte Alegre, GO), Vicente Pirez (DF), University of Brasília (DF), and in the State University of Campinas (SP), distances ranging from 2000 to 50 km (Fig. 1). We analyzed 450 recordings including a recording of *O. manilata* from Nova Floresta (MT) attained from the Fonoteca Neotropical Jacques Vielliard (Unicamp, Brazil).

We used in the analysis 3 individuals per species and

Figure 1. Map depicting the localities of the recordings of parrots used in the current study.

3 recordings per individual. We performed two replicas, each one in a different location, totaling 18 flight calls per species. This allowed us to include individual and populational variation. However, we were not able to record or obtain this number of samples with good quality for all species. For this reason, we used a smaller sample size for *A. ararauna* (10 calls from a single location), *P. leucophthalma* (7 calls from 2 locations), *P. maximiliani* (7 calls from a single location), and *O. manilata* (5 calls from 2 locations).

Sound analysis

Calls were chosen based on signal-to-noise ratio. We filtered the selected recordings with a high pass filter (100Hz) and normalized the intensity to 0 dB. We edited sound files using Cool Edit Pro (Syntrillium Software, USA) (512 FFT size, Blackmann-Harris function: 70% window size) before we measured 11 distinct call parameters (Fig. 2): Call duration (s), initial and final fundamental frequencies (Hz), minimum and maximum fundamental frequencies (Hz), the time in which the call achieve its maximum and minimum fundamental frequencies (s), net modulation of the call (final minus initial fundamental frequencies; Hz), fundamental frequency band (Maximum minus minimum fundamental frequency values; Hz), dominant frequency (frequency presenting the highest energy; Hz), and the number of fundamental frequency local maxima. We performed a cross correlation analysis using the software Sound Ruler (Marcos Gridi-Papp (UCLA, USA)), which was also used to make the sonograms (512 FFT size).

Statistics

In order to test the spectrum partition hypothesis in which a low degree of frequency overlap is expected between species, we used a Kruskal-Wallis with a Dunn *a posteriori* test to check for pairwise differences in the dominant frequency. Using the 11 variables measured we performed a principal component analysis (PCA) to visually evaluate species segregation, by considering the resulting figure as a proxy of the acoustical space.

We used a multinomial regression to classify the calls species based on vocal parameters. If the calls are indeed species-specific signals we expect an efficient species classification based call parameters. Preceding the multinomial analysis, we examined the existence of collinearity among call parameters by calculating the variance inflation factor (VIF) and dropping the covariate with the highest VIF. We recalculated the VIFs and repeated the process until all VIFs are smaller than 3 (Zuur *et al.* 2010). The full list of the parameters kept in the model for is presented in Table 1 (the full model).

We selected candidate models based upon a stepwise approach in which we compared a full model (with all variables included) against partial models built by suppressing a single variable (please see Magroski *et al.* 2017). We used second-order Akaike's information criteria (AIC_c) to make the selection (lowest AIC_c), and permanently removed the suppressed variable from the model. The selected model was then used as base model in the next round, which further suppressed variables,

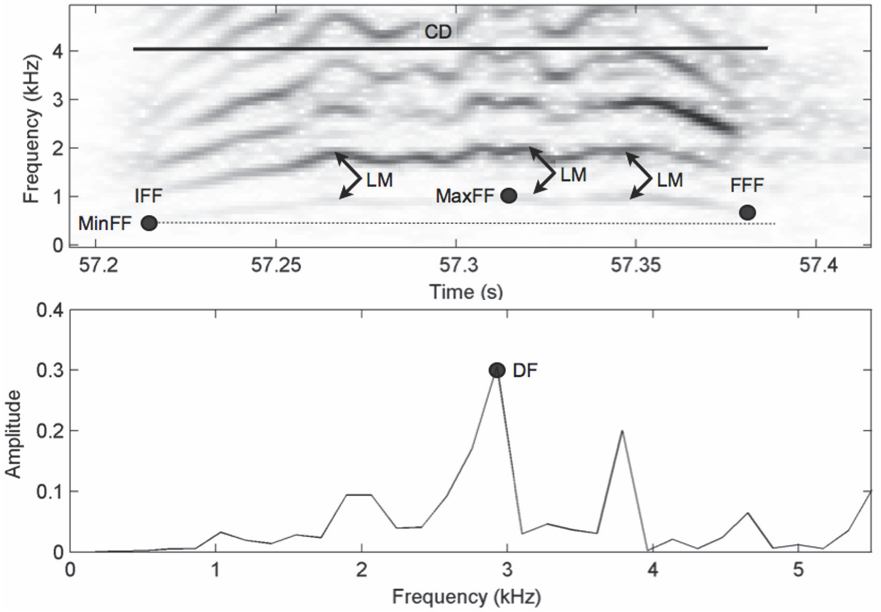

Figure 2. Sonogram and power spectrum of a *Diopsittaca nobilis* flight-call, showing the directly measured parameters: CD - Call duration; IFF - initial fundamental frequency; FFF - final fundamental frequency; MFF - minimum fundamental frequency; MaFF - maximum fundamental frequency; TminFF - the time in which the call attained its minimum fundamental frequencies; TmaxFF - the time in which the call attained its maximum fundamental frequencies; DF - dominant frequency; LM - fundamental frequency local maxima.

one at a time. We repeated this process until the best model was the one built without the removal of any additional variable. We compared the AIC$_c$ value of the candidate models (the full model and base models of each round) to a null model to select the final models. As low differences in AIC$_c$ values indicate support for multiple models (Burnham *et al.* 2011), we kept the models with ΔAIC$_c$ scores lower than 4, and tested if they hindered higher classification efficiencies. The multinomial models were built using R software (R Core Team 2015) with the nnet package (Ripley & Venables 2011), while the models were selected by using the AICcmodavg package (Mazerolle 2011).

We used a cross correlation analysis (CCA) to calculate similarity indexes, which are calculated from the sonograms on the basis of the pair-wise acoustical energy overlap. We used the similarity indexes to test whether the similarities within species were higher than similarities between species. We used a Mann-Whitney non-parametric test to examine the differences.

In order to investigate the influence of phylogeny we made a phenetic analysis using the acoustic parameters, and compared the results to published parrot trees (Tavares *et al.* 2006, Wright *et al.* 2008). The phenetic analysis was implemented in Fitopac statistical package (George Sheperd, UNICAMP, Brazil), by which we grouped the calls based on the Euclidean distance through an UPGMA procedure, as originally proposed by Slabbekoorn *et al.* (1999).

RESULTS

Flight-calls

Parrot flight-calls are very diverse showing differences both at the temporal and spectral domain (Fig. 3, Table 1), presenting variations in harmonic, tonal and modulation patterns (Fig. 3). In terms of spectrum, most of the species call's overlap, mostly due to a broad bandwidth use of the frequency spectrum, from 0.5 kHz to 6 kHz (Table 1). The dominant frequency exhibited wide variations within species (for most species studied) and a considerable overlap between species. Only few pairwise comparisons revealed differences in dominant frequencies contradicting the expectations regarding the spectral partition hypothesis (Table 2, Fig. 3).

The results of the PCA show that both temporal and spectral components contributed to the dispersal of species along root 1 (59% of the variation) and the number of local maxima and the time to reach the minimum frequency along the root 2 (16%). There is little overlap in the acoustical space and species visually segregate. Nevertheless, species such as *P. leucophthalmus* (Ple), *E. aurea* (Eau) and *O. manilata* (Oma) displayed limited overlap (Fig. 5).

We found empirical support for two multinomial models (AIC$_c$ < 4; Table 3). While the best model correctly classified 95% of the calls the second best model, which presented a ΔAIC$_c$ of 2.2 (Table 3), conveyed a perfect species classification (100% correct; table 4), supporting the idea of species-specific flight-calls.

Within and between species flight-call similarity

The results showed above were confirmed and complemented by a Cross Correlation Analysis (CCA). The average call similarity index differed between species (Table 5), and similarities are higher within species than between species (Table 5). Calls of Aar, Dno and Oma showed higher inter-specific similarities (0.4) while Axa, Bch and Fxa showed lower interspecific inter-specific

Table 1. Flight-call parameters. Data is presented as mean (variation coefficient) *n* – sample size, MinFF – minimum fundamental frequency, MaxFF – maximum fundamental frequency, FFBW – fundamental frequency bandwidth, dF – dominant frequency, No. max – number of local maxima; Aae – *Amazona aestiva*; Aar – *Ara ararauna*; Eau – *Eupsittula aurea*; Ple – *Psittacara leucophthalmus*; Axa – *Alipiopsitta xanthops*; Bch – *Brotogeris chiriri*; Dno – *Diopsittaca nobilis*; Fxa – *Forpus xanthopterygius*; Oma – *Orthopsittaca manilata*; Pma – *Pionus maximiliani*.

Species	No. of locations	*n*	Duration (ms)	MinFF (Hz)	MaxFF (Hz)	FFBW (Hz)	dF (Hz)	No. max
Aae	2	18	311 (7%)	418 (9%)	2457 (7%)	2030 (8%)	2255 (39%)	2.5 (25%)
Aar	1	10	343 (38%)	292 (16%)	798 (22%)	506 (36%)	2472 (30%)	4.7 (57%)
Eau	2	18	197 (19%)	693 (16%)	1654 (13%)	962 (19%)	4310 (8%)	5.9 (21%)
Ple	2	7	211 (7%)	660 (14%)	2951 (7%)	2291 (12%)	3223 (16%)	6.9 (32%)
Axa	2	18	205 (8%)	512 (18%)	2931 (29%)	2419 (36%)	2305 (5%)	2.7 (3%)
Bch	2	18	125 (10%)	1107 (13)	4551 (12%)	3444 (16%)	4478 (10%)	4.3 (19%)
Dno	2	18	194 (11%)	449 (18%)	1117 (7%)	669 (13%)	3130 (30%)	9 (22%)
Fxa	2	18	98 (22%)	1599 (18%)	6932 (5%)	5333 (8%)	4838 (8%)	3.9 (31%)
Oma	2	4	153 (7%)	302 (9%)	1851 (11%)	1549 (12%)	3514 (23%)	3.8 (29%)
Pma	1	7	136 (3%)	636 (13%)	3584 (3%)	2947 (2%)	3149 (6%)	3.6 (15%)

Table 2. Results of pairwise Bonferroni-corrected Dunn *a posteriori* test comparisons of the dominant frequencies. Bold values highlight significant differences. Species codes as in Table 1.

	Aae	**Aar**	**Eau**	**Ple**	**Axa**	**Bch**	**Dno**	**Fxa**	**Oma**	**Pma**
Aae	1									
Aar	1.000	1								
Eau	**<0.001**	**0.002**	1							
Ple	1.000	1.000	1.000	1						
Axa	1.000	1.000	**<0.001**	0.755	1					
Bch	**<0.001**	<0.001	1.000	0.421	**<0.001**	1				
Dno	0.474	1.000	0.062	1.000	0.284	**0.011**	1			
Fxa	**<0.001**	**<0.001**	1.000	**0.034**	**<0.001**	1.000	**<0.001**	1		
Oma	0.976	1.000	1.000	1.000	0.722	1.000	1.000	0.260	1	
Pma	1.000	1.000	0.798	1.000	1.000	0.302	1.000	**0.022**	1.000	1

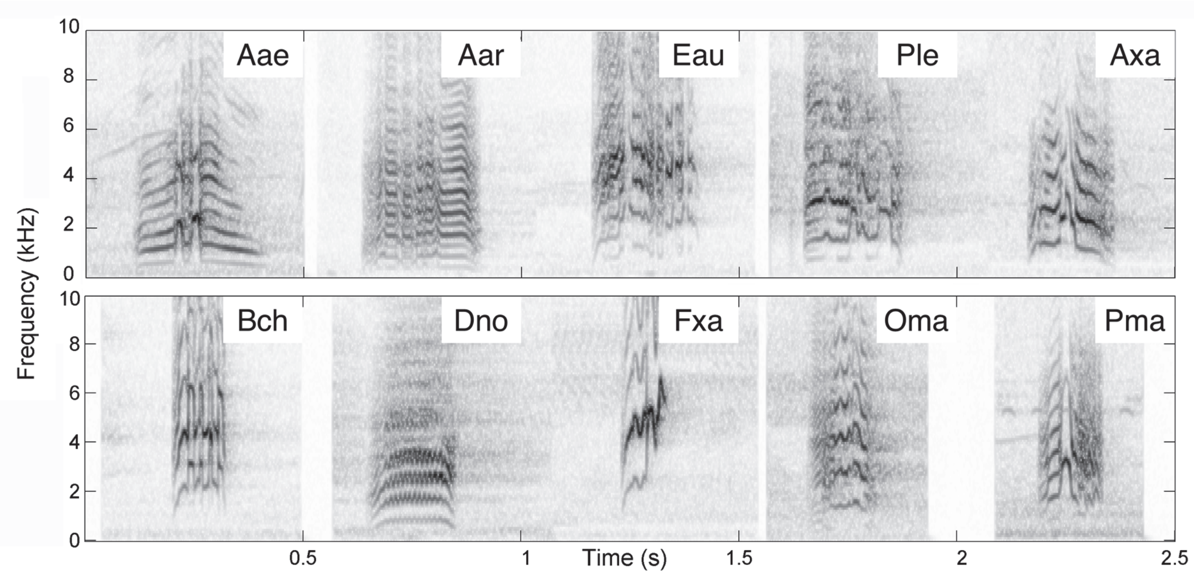

Figure 3. Flight-calls of the 10 parrot species studied (FFT 512, hamming window, 30% window size). Species codes as in Table 1.

indexes (< 0.30). Within species, similarity varies from 0.70 (in Aae, Aar, Pma) to 0.42 in Bch.

Species relatedness

The phenetic analyses show a grouping pattern in which two major groups are formed (Fig. 6). The first one comprises the Macaws (Aar, Dno and Oma) and also Eau. The second group comprises the Parrots (Pma, Aae and Axa, but also Ple). Both, Fxa and Bch have been positioned outside these two major groups.

DISCUSSION

Our results showed considerable structural differences among parrot's flight-calls, which suggest the existence of species-specific information coded within in the signal. Regarding dominant frequencies, the presence of overlapping frequencies does not support the spectrum partition hypothesis. In general, vocalizations are short in duration, possess a broad bandwidth and harmonic structure, and are frequency modulated. These call characteristics are well suited for a long-range communication that may reach up to a kilometre in some parrot species (de Araújo 2011).

Calls with complex structures such as quick modulations and harmonic structures can encode large amounts of information (Lohr *et al.* 2003). Even thought complex environments difficult information flow, these signals are well suited for open habitats such as Cerrado, which presents low signal degradation (Chapuis 1971, Morton 1975). Long distance communication is especially important to this group of gregarious species, as they forage in wide areas with dispersed food patches. They form small foraging groups during the day (de

Table 3. Multinomial regression model selection for recorded species of parrots in relation to call parameters. Vocal parameters: MaFF - maximum fundamental frequency; MiFF - minimum fundamental frequency; DF - Dominant frequency; mod - net frequency modulation (final minus initial fundamental frequencies; Hz); LM - number of fundamental frequency local maxima. K - number of parameters; AIC_c - second-order Akaike's information criteria; ΔAIC_c - variation in AIC_c to best model; Wi - Akaike's weight.

Model (Species ~)	K	AIC_c	Delta_AIC_c	Wi
MaFF + mod	27	96.5	0.0	0.75
MaFF + mod + DF	36	98.6	2.2	0.25
MaFF + mod + DF + LM	45	135.5	39.0	0.00
MaFF + TminFF + mod + DF + LM	54	180.4	84.0	0.00
MiFF + MaFF + TminFF + mod + DF + LM	63	236.5	140.0	0.00
Null	9	626.5	530.1	0.00

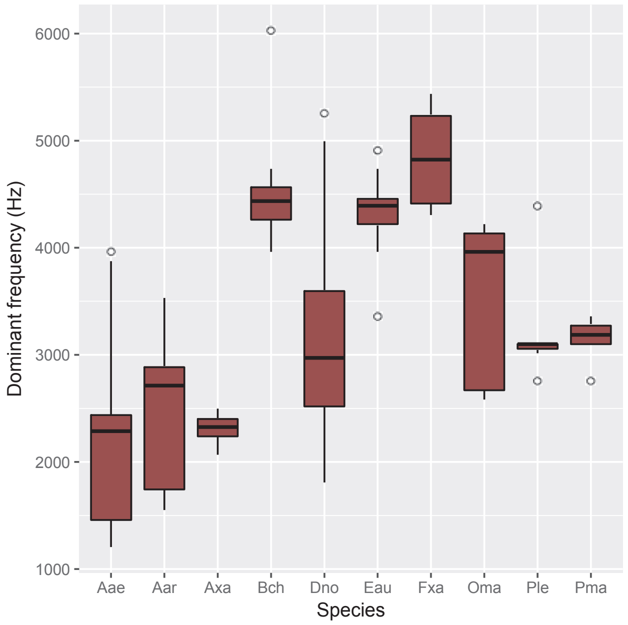

Figure 4. Graph of the median and quartiles of the dominant frequencies of the flight-calls of the 10 parrot species studied, showing high spectral overlap between most species.

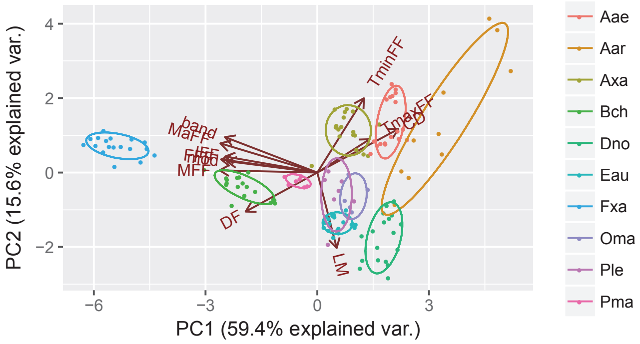

Figure 5. Principal component analysis (PCA) of analysed flight-calls depicting the structural differences among acoustical parameters. Species codes as in Table 1.

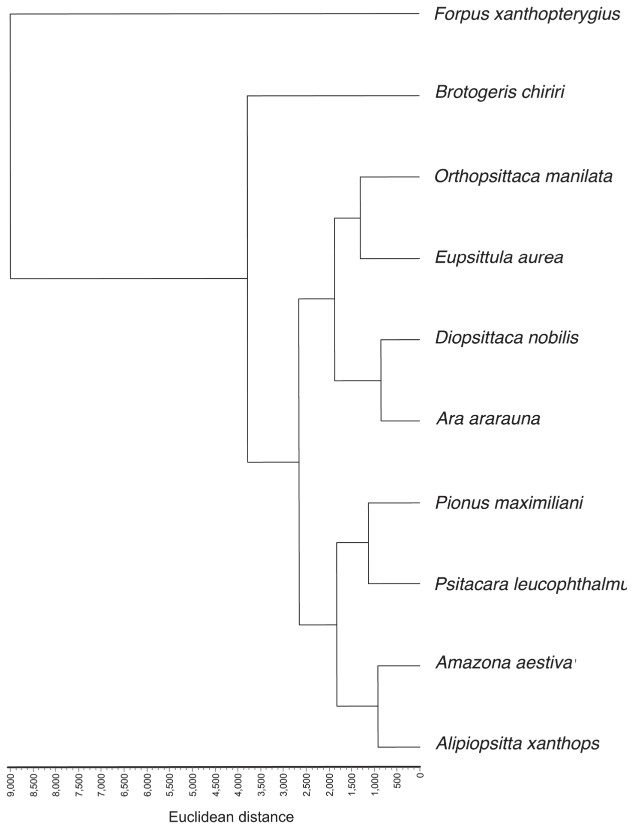

Figure 6. Phenetic analysis of the species based on average flight-call parameters (UPGMA, Euclidean Distance).

Araújo 2011, de Araújo & Marcondes-Machado 2011) that congregate at dusk to roost within larger flocks (Carrara *et al.* 2007, de Araújo *et al.* 2011). Because of such flock dynamic, it is important for Parrots to maintain group cohesion by regularly emitting long-range acoustic signals, such as the flight-call (de Araújo 2011, de Araújo *et al.* 2011).

Our results show a clear partition among species within the acoustical space, in which spectral and temporal parameters are main responsible factors. Species-specific acoustic signals are common in nature, but the particular call parameters that contribute to specificity should vary depending on the species life history, genetics and the acoustics of the environment. For migratory passerines, flight-calls are species-specific and are used to maintain cohesion in large groups (Farnsworth 2005). Within the Parrots species studied three parameters were enough to allow for the correct classification of 100% of the calls. Call

Table 4. Confusion table presenting the number and percentage of correct classifications, which depicts the performance of the two multinomial models used. Model 1 - Species ~ MaFF + mod; Model 2 - Species ~ MaFF + mod + DF; where: MaFF - maximum fundamental frequency; DF - Dominant frequency; mod - net frequency modulation (final minus initial fundamental frequencies; Hz). Species codes as in Table 1.

Species	**Sample size**	**Model 1**		**Model 2**	
		Correct	**%**	**Correct**	**%**
Aae	18	17	94	18	100
Aar	10	10	100	10	100
Axa	18	18	100	18	100
Bch	18	17	94	18	100
Dno	18	18	100	18	100
Eau	18	16	89	18	100
Fxa	18	18	100	18	100
Oma	5	5	100	5	100
Ple	7	5	71	7	100
Pma	7	6	86	7	100
Total	**137**	**130**	**95**	**137**	**100**

Table 5. Cross correlation (CCA) similarities indexes ± standard deviation. I - number of the individuals, *n* - within group sample size; *N* - between group sample size. Species codes as in Table 1.

Species	**I, *n*, *N***	**Similarity Within species**	**Index Between species**	**Z(U)**	***P***
Aae	6, 153, 2142	0.70 ± 0.10	0.36 ± 0.12	20.42	< 0.0001
Aar	3, 45, 1270	0.69 ± 0.06	0.40 ± 0.06	11.09	< 0.0001
Eau	6, 153, 2142	0.53 ± 0.08	0.37 ± 0.08	17.3	< 0.0001
Ple	3, 21, 910	0.50 ± 0.07	0.36 ± 0.11	5.41	< 0.0001
Axa	6, 153, 2142	0.63 ± 0.12	0.29 ± 0.13	19.79	< 0.0001
Bch	6, 153, 2142	0.42 ± 0.11	0.30 ± 0.10	12.83	< 0.0001
Dno	6, 153, 2142	0.60 ± 0.06	0.41 ± 0.11	18.51	< 0.0001
Fxa	6, 153, 2142	0.49 ± 0.12	0.25 ± 0.10	18.79	< 0.0001
Oma	2, 10, 653	0.64 ± 0.10	0.40 ± 0.09	4.99	< 0.0001
Pma	3, 21, 910	0.72 ± 0.08	0.39 0.12	7.73	< 0.0001

similarities confirmed these results, as we found that call similarity was always higher within species than between species, what supports the idea of flight-calls to be responsible to encode species-specific information at long-range.

Intraspecific similarity seems to depend upon the function of the flight-call as well as its usage by each species. If in the one hand species-specific recognition signals should be a highly stereotyped signal with little variation on the acoustic parameters, on the other, if it also encodes information on individuals or groups, it should present higher variation due to the parameter variation necessary to encode such individual or populational information. In this context, higher similarities would lead us to assume the existence of stereotyped species-specific signals used in communication contexts in which species identity is sufficient (Collins 2004), while a lower intraspecific similarities should be associated with conveying information other than species signature, which might contain information on groups (Wright 1996, Wright *et al.* 2008) or individuals (Wanker *et al.* 1998, Berg *et al.* 2011, Marques *et al.* 2011).

Structural differences in flight-calls could have an important role in regulating the social interactions within the social group (Balsby & Adams 2011), by conveying for example information on individual identity or motivation (Bradbury & Vehrenkamp 1998, Berg *et al.* 2011). Most species presented high similarities within species (> 0.5), but call similarity varied greatly between species, from 0.70 in *A. aestiva* to 0.42 in *B. chiriri* (Table 2). We expect high intraspecific similarity to be less associated to social bonds, leading to social groups that are formed casually with low flock composition stability (Berg *et al.* 2011). In fact, some species, such as *A. aestiva*, *A. xanthops* and *P. maximiliani* showed a remarkable amount of intraspecific similarity, while showing low coefficients of variation. Species such as *A. xanthops* or *A. hyacinthinus* presents flight-calls so stereotyped that hindered the possibility of identifying individuals acoustically (de Araújo 2007, Ueno 2007).

Nevertheless, most (if not all) of the parrot species studied are extremely social, an apparent pattern for Neotropical parrot species (Rasmussen 1999, Carrara 2007, de Araújo 2011, de Araújo *et al.* 2011). Hence, even though some of the studied species showed highly stereotyped flight-calls, given Parrot repertoire size it would not be surprising if Parrots encode information on individual and groups within other calls (*e.g.* de Araújo *et al.* 2011, Moura *et al.* 2011). Is such species, while flight-call would be responsible to convey species-specific species at long ranges, shorter range calls could act as the carrier of social information.

Ara ararauna is a special case in which we found a high degree of similarity but also a high coefficient of variation in some non-spectral parameters. While these variations seem not affect the species-specificity, it could contribute to coding additional information within flight-calls. Overall, our results suggests that the Macaw's flight call can potentially encode information on individual and/or group (Cortopassi & Bradbury 2006) and simultaneously convey information on species identity.

Nonetheless, some species exhibited low levels of similarity that could be associated with information other than the species signature (see above). Some studies showed that flight-calls in species like *Forpus conspicillatus*, *F. passerinus* and *Eupsittula canicularis* possess individual characteristics useful to determine the identity of the caller, or to address the message to a specific group member (Wanker *et al.* 2005). In this sense, a similar process could explain the low levels of intraspecific call similarity observed in *F. xanthopterygius, E. aurea and P. leucophthalma*, making them good candidates for future studies of flight-call variation, individual signatures, and vocal evolution.

In spite of the high intraspecific variation observed, the phenetic tree suggests that flight-calls can still retain considerable phylogenetic information. The acoustical structure seems to reflect the phylogenetic relationship between the studied species, and even though Parrots show socially learned calls with much variation (Margroski *et al.* 2017), flight-calls can still provide important phylogenetic information (Vielliard 1994). The comparison of our results to published phylogenies (Tavares *et al.* 2006, Wright *et al.* 2008) partially agrees with the species division in two groups, the first one comprising the Macaws and parakeets (long-tail) and the second one formed by parrots (short-tail), in addition to the parakeet species *P. leucophthalma*. Additionally, *B. chiriri* and *F. xanthopterygius* were placed outside these two major groups in our analysis, even though in published phylogenies they form a close related group with the other two clades (Tavares *et al.* 2006, Wright *et al.* 2008). Additionally, *P. leucophthalma* was grouped with parrots and not with the macaws. Its strange position may be explained by the noise coming from the high intra-specific variation.

Our results suggest flight-calls as species-specific signals that contain considerable information on phylogeny. Even though flight-calls can be important for signalling species identity at long-ranges, some parrot species may still use it in other communication contexts that include information on group and individual identities.

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