Bibliographical reference

Short-Term Variations of Dialects in Short Songs of Two Species of Colonial Caciques (Cacicus), Hélène Thieltges, Laurence Henry, Véronique Biquand and Pierre Deleporte, Acta Acustica **vol. 100** (Number 4), 2014, pp. 759-766

DOI
https://doi.org/10.3813/AAA.918755

ACTA ACUSTICA UNITED WITH ACUSTICA
Vol. 100 (2014) 759 – 766

DOI 10.3813/AAA.918755

Short-Term Variations of Dialects in Short Songs of Two Species of Colonial Caciques (Cacicus)

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Summary
The vocalizations involved in social communication of many oscine species present dialectal variants in vocalizations involved in social communication. Different hypotheses predict the function of these dialects: the "local adaptation" hypothesis, the "social adaptation" hypothesis and the "epiphenomenon" hypothesis. The social adaptation hypothesis predicts a rapid change in local dialects adjusted to each colonial variant via vocal sharing of constantly drifting song types. Here we investigated the dialect temporal variations of two colonial Cacicus species as we know that spatially-restricted dialectical variants, probably linked to social organization, exist in these species. Sound recordings were collected in the field, focalising on a series of nesting colony trees followed over several years. Songs were analysed from sonograms and their temporal and frequency parameters were compared. The fact that we observed short-term variations of colonial dialects tends to support the hypothesis of a culturally acquired colony-specific vocalization in both species.

PACS no. 43.80.-n

1. Introduction

The term "dialects" was first applied to geographical variations of bird songs in the early sixties [1], and song birds still remain a particularly relevant model for studying animal vocal communication plasticity. Mundinger [2] defined dialect as "a variant song tradition shared by members of a local population of birds, with a dialect boundary delineating it from other variant song traditions". Studies of dialect stability have focused on several groups of higher vertebrates, and a number of distinct patterns of dialect stability have been reported. In some cases dialects appear to be both geographically and temporally stable (killer whales [3], white-crowned sparrows [4], Darwin's finches [5], mountain white-crowned sparrows [6], white-crowned sparrows [7]). In other cases acoustic forms are more temporally variable, with new call forms being introduced into populations and others being lost (chickadees [8], chaffinches [9], indigo buntings [10]). In still other cases, some components of a vocal signal have been found to remain stable while others change with time, suggesting that different components may be governed by different forms of selection (starlings [11], white-crowned sparrows [12]).

Authors repeatedly attempt to decipher the functions of animals' dialectal variations [13, 14, 15, 16, 17, 18], but no satisfactory model seems to cover the full range of variations for all species. Payne's models [14] remain a basic reference even for recent reviewers [15], with three possibilities: the "local adaptation" hypothesis (see also [13]) that "posits that females gain fitness advantages when they are able to mate with males from their natal regions, in preference to males from other regions"; the "epiphenomenon" hypothesis (dialects are by-products of song learning abilities and dispersal, see also [16, 18, 19, 20]), and the "social adaptation" hypothesis (dialectal areas would correspond to social entities [14, 21, 22, 23]). Currently, none of these hypotheses can be either favoured or disqualified on a general basis, but attempts can be made to examine their potential validity at a species level. One way to test these hypotheses is to study the stability of these vocal dialects over time, i.e. to analyse how songs differ from year to year in a particular location. The local adaptation hypothesis predicts that dispersing birds tend to settle more than would be expected by chance in sites where conspecifics sing their natal dialects, than in sites where conspecifics sing "foreign" dialects. The social adaptation hypothesis predicts that individuals learn new vocalizations when dispersing to a new dialect area, and match (mimic) vocalizations in that new locality [14].

Yellow-rumped caciques, *Cacicus cela*, are among the very first song birds, and one of the few neotropical species, for which dialectal variations have been described [21, 23, 24, 25, 26]). Recently, the presence of local dialects in *C. cela*'s short songs was confirmed, and similar

Received 3 January 2014,
accepted 5 March 2014.

spatial patterns of vocal variations in the closely related red-rumped cacique *C. haemorrhous*'s specialised short songs were described (Thieltges et al., unpublished data). *C. cela* is also the first species for which a strong link between "social requirements" and dialectal variations has been suggested [21, 24]. Both these species colonize year after year the same localities, and this makes them good models to study the stability of dialects over time.

In the present study, we hypothesized that if dialects in yellow-rumped caciques and red76 rumped caciques have a social adaptation function, local dialects should change rapidly (on a year-to-year basis, incompatible with simple genetic drift). Such fast evolving dialects would result from the rapid convergence of song structure and vocal drift as song variants are copied from one bird to another, a trait that can be called cultural variation.

To test this hypothesis, we recorded in the field the specialized short songs emitted by males of two species of colonial breeders, *C. cela* and *C. haemorrhous*, in French Guyana. We analysed their repertoire at nesting colonies and compared songs from the same site at different times, to study year-to-year changes.

2. Material and methods

2.1. Study area

We recorded vocalizations of *C. cela*'s and *C. haemorrhous*'s colonies from the beginning of October to mid-December, from 2005 to 2012 (exceptions: recordings were made in June 2005 and no recordings were made in 2011) in French Guiana, during the dry season when both species typically breed [27]. The recordings were made between 0600h and 1300h (EST). We found both species nesting in colonies in trees isolated from the surrounding more densely wooded habitat. Occasionally the two species were nesting on different branches of the same colony tree as described by Jaramillo and Burke [28]. Nesting colonies are regularly established in the same or a neighbouring tree year after year.

2.2. Subjects

Both *C. cela* and *C. haemorrhous* are colonial breeders with dense colonies ranging from a few to several dozen nests, and occasionally the two species breed in the same tree. These two colonial species live in mixed multi-male and multi-female social groups, both at nesting colony sites and at collective roosting places [28, 29]. Cacique colonies are composed on average of 20 females or nests, every female building a unique nest during a "breeding session" in a shared colonial tree [29]. During the building of the nests and before incubation, *C. cela*'s sex ratio is 1 male:2 females and C. haemorrhous's is 1 male:1.5 female (males may temporarily outnumber females with sex ratios reaching 0.6/0.8 [29]). Caciques often return to the same trees for breeding [29]. Since birds could not be caught easily and colour-ringed individually, our data are based on "colony communal data" where all recordings of the males were considered together. Nevertheless, some individual males could be followed continuously by sight for up to 20 minutes. Observations and listening in the field and analysis of sonograms of short songs from different colonies amply supported the presence of local dialects, but this study focused on the *C. cela* and *C. haemorrhous* colonies that included at least two different clearly identified males whose recordings were retained for further analysis. We analysed six songs per colony, choosing them from as many different individuals as possible. For this, we analysed one song from 2 to 4 different identified males, as well as songs randomly taken from recordings of males of uncertain identity.

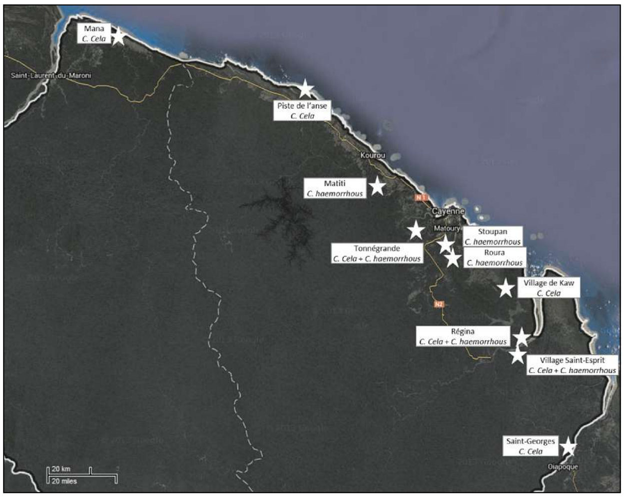

Figure 1. Study sites in French Guiana.

2.3. Sound recording

Vocalizations were recorded using a digital sound recorder Marantz PMD670 and an omni-directional mono stick microphone with a 65cm-diameter directional parabola. Birds were recorded from a distance estimated at 12 to 30 meters. The geographical position of each colony was GPS recorded with a Pocket PC DigiWalker Mio 168 and CartoExplorer3 (Bayo) software using the detailed IGN maps of French Guiana for geographical position control. We made the observations during the breeding season when singing activity and presence of numerous males peak. These species present a strong sexual dimorphism so we could identify adult males easily (they are much larger than females). We analysed *C. cela*'s short songs from 7 sites and *C. haemorrhous*'s from 6 sites for which we had recordings from the same locality for at least two different years (Figure 1, Table I and II).

2.4. Acoustic analyses

All recordings in WAVE format were analysed by using a PC with the customized ANA sound analysis software [30]. Sonograms were made with Fast Fourier Transformation (FFT) using a 256-point Hanning window and a 128-point step. Sampling frequency was 22 kHz and pixel

Table I. *C. cela* colony sites and year of study.

	2005	2006	2007	2008	2009	2010	2012
Mana						x	x
Piste de l'anse						x	x
Tonnégrande	x	x		x			
Village de Kaw				x	x	x	
Régina				x		x	x
Village Saint-Esprit			x	x			
Saint-Georges						x	x

Table II. *C. haemorrhous* colony sites and year of study.

	2005	2006	2007	2008	2009	2010	2012
Matiti					x	x	
Tonnégrande	x	x	x	x			x
Stoupan				x	x	x	
Roura				x	x	x	
Régina				x	x	x	x
Village Saint-Esprit			x	x			

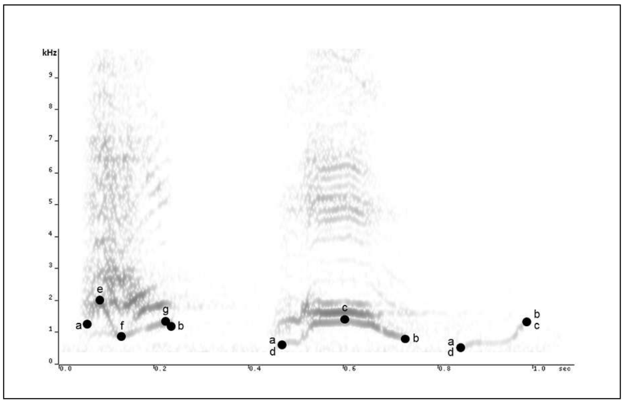

Figure 2. *C. cela* short song. Measures made on the four notes of the typical song sequence (numbered 1 to 4 below the figure). a: beginning frequency (Fbeg); b: end frequency (Fend); c: maximal frequency (Fmax); d: minimum frequency (Fmin); e: frequency at the first inflexion point (Finfl1); f: frequency at the second inflexion point (Finfl2); g: Frequency at the third inflexion point (Finfl3).

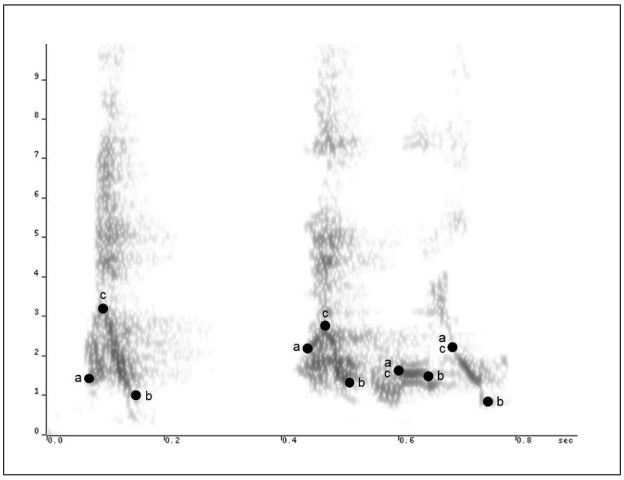

Figure 3. *C. haemorrhous* short song. Measures made on the four notes of the typical song sequence (numbered 1 to 4 below the figure). a: beginning frequency (Fbeg); b: end frequency (Fend); c: maximal frequency (Fmax).

size 87 Hz × 11.5 ms. All vocalizations include harmonics, but since the maximum energy was on the fundamental frequency, measures were made on fundamental frequency parameters. As the first note of *C. cela*'s short songs is not always present we decided to discard the data for this note from the analyses (but it is structurally very similar to the second note, just like the two first notes of *C. haemorrhous*'s short song). We measured the following frequency parameters for *C. cela*'s short songs at homologous points: frequency at the beginning (Fbeg) and at the end of each note (Fend), intermediate frequency at the three inflection points of the first note (FinflX), and maximum (Fmax) and minimal intermediate frequency (Fmin) of the following notes (Figure 2). We also measured the following temporal parameters: duration of each note (XTtot 2, 3, 4), timing of the three inflection points of the first note (TFinfle, f, g), timing of maximal and minimal frequencies (TFmax, TFmin) and total duration of the short song (Ttot). We also took frequency measurements on homologous points for each note of *C. haemorrhous*'s short songs and measured the temporal parameters (Figure 3).

2.5. Statistical analysis

We analysed the acoustic properties of *C. cela*'s and *C. haemorrhous*'s songs in relation to their locality of emission by a Partial Least Squares – Discriminant Analysis (PLS-DA [31]. We preferred this multivariate analysis to a Linear Discriminant Analysis [32] as the number of explanatory variables was nearly equal to or greater than the number of individuals [33]. The number of components required for each model was determined by cross-validation, based on the M-fold method with 10 groups

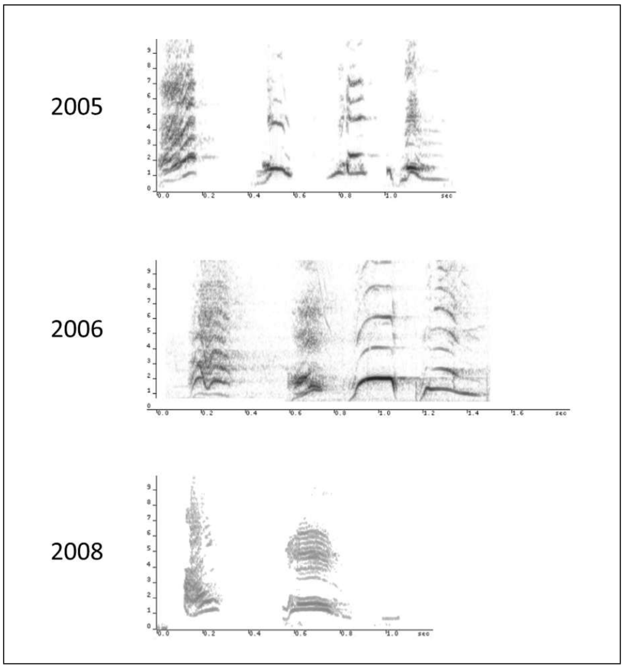

Figure 4. *C. cela*'s sonograms of the dialects on successive years at the Tonnégrande locality.

and 20 repetitions [34]. The importance of each variable for discrimination of spatial sites was estimated by using VIP scores [35]. This is a weighted sum of squares of the PLS-weights, with the weights calculated from the amount of Y-variance of each PLS component. All statistical analyses were performed by using the R software [36] and the additional package 'mixOmics' [37].

3. Results

Our results showed that each year the short songs of both species revealed local dialects. The dialects of male *Cacicus cela*'s short songs, recorded at different sites, clearly differed among years, for all sites considered. Figure 4 shows the example of dialect sonograms for successive years at the Tonnégrande locality. Many parameters present significant differences (note 1: frequency and timing at the first inflection point, duration of the first note; note 2: maximal and ending frequencies, timing of the maximal frequency; note 3: beginning and ending frequencies, timing of the maximal and minimal frequencies).

We present our detailed results for three sites: Tonnégrande, Village de Kaw and Régina, for which we have recordings for a maximum number of years (Figure 5a,b,c).

The changes observed in short songs concern many acoustic parameters but not always the same ones (Table III).

A similar analysis questioned whether some dialects were simply found at other sites another year, for example whether the Stoupan 2008 dialect was emitted in Village de Kaw in 2009, as if a whole group with a stable dialect had simply gone to another site, but no such pattern could be evidenced for all sites and years studied (supplementary material 1).

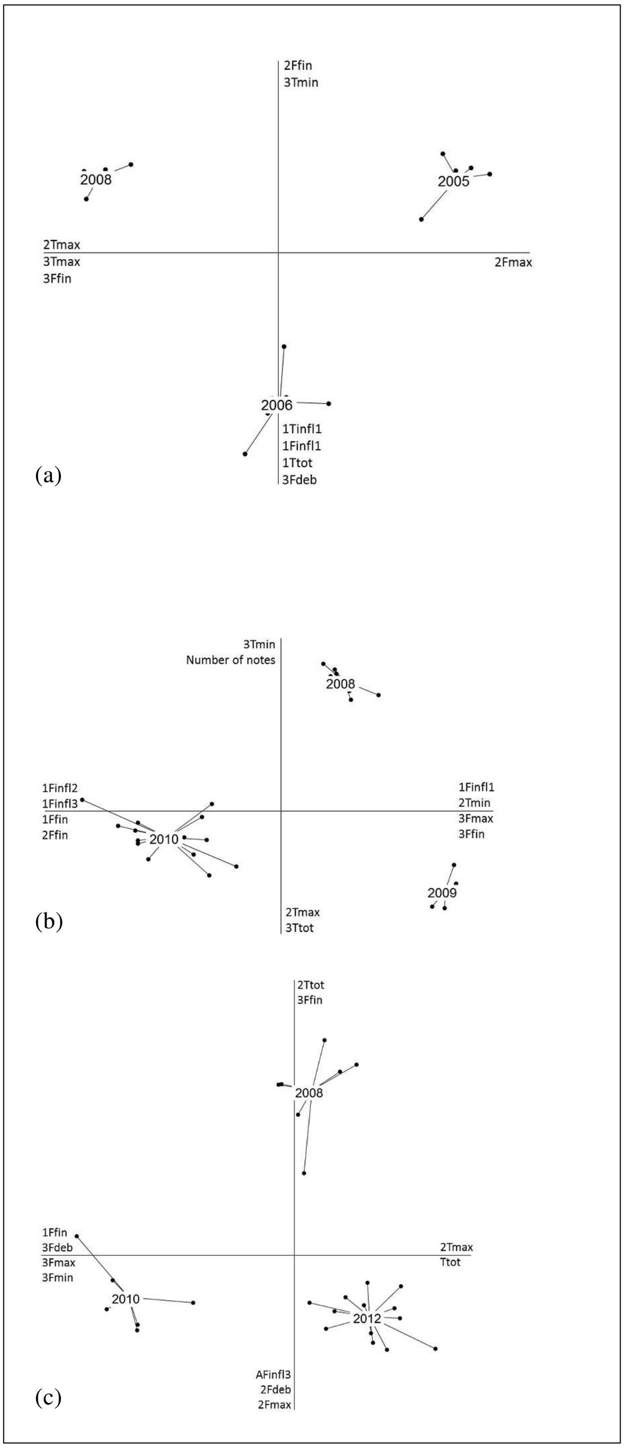

Figure 5. *C. cela* short songs. Two-dimensional PLS-DA graph of songs. Each point represents a short song. Abbreviations on X and Y axes = acoustic parameters with VIP>1 (determinant in the differences observed). Parameter abbreviations are preceded by the measured notes' numbers. Location a = Tonnégrande, b = Village de Kaw, c = Régina.

We also evidenced dialects in male *Cacicus haemorrhous*'s short songs each year and they differed among years at all the sites studied. Figure 6 shows the example

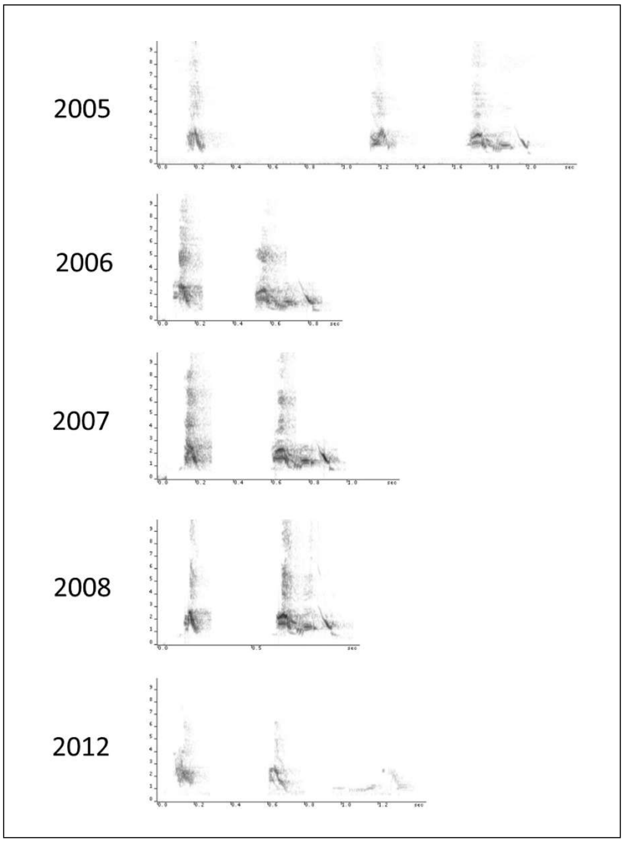

Figure 6. *C. haemorrhous*'s sonograms of the dialects on successive years at the Tonnégrande locality.

of dialect sonograms for successive years at the Tonnégrande locality. Many parameters present significant differences (note 1: maximal and ending frequencies; note 2: ending frequency; note 3: maximal and ending frequencies; note 4: ending frequency and total duration). However, differences seem somewhat less contrasted than for *C. cela* (Figure 7a,b,c,d). The dialects recorded at Régina in 2009 and 2012 are quite similar; however, recordings revealed stronger differences between 2008, 2009 and 2010 (Figure 7c). Similarly recordings made at Roura presented differences between 2008 and 2009 and between 2008 and 2010 (Figure 7d), while the dialectal variants' recordings made at Tonnégrande presented less marked differences between 2006 and 2008 than between 2005 and 2012 (Figure 7a). Dialectal differences appear, lesser in this species than in *C. cela*; nevertheless, we never found exactly the same variants twice at any of the sites studied in *C. haemorrhous*.

As for *C. cela*, we could not identify any particular song parameters that could characterize any of the dialects. Acoustic features also changed from year to year for a given site (Table IV). A similar analysis questioned whether some dialects were simply found at another site another year, for example whether the Stoupan 2008 dialect was emitted at Village de Kaw in 2009, as if a group with a stable dialect had simply gone to another site, but no such pattern could be evidenced for all sites and years studied (supplementary material 2).

Table III. *C. cela* acoustic parameters implied in differences between groups (years) (i.e. VIP>1) ranked by order of importance according to their VIP scores.

Mana	1Ttot	Ttot
	2Fmax	1Fbeg
	1Fend	Number of notes
	1Tinfl1	3Fmin
	1Finfl2	1Finfl3
	1Tinfl2	
Piste de l'anse	1Finfl2	2Fmax
	3Fend	3Ttot
	1Tinfl3	3Fmax
	1Ttot	1Tinfl2
	1Finfl3	3Tmin
	1Tinfl1	
Tonnégrande	1Finfl1	1Tinfl1
	1Ttot	3Tmax
	3Fbeg	3Fend
	2Fmax	3Tmin
	2Fend	2Tmax
Village de Kaw	3Tmin	1Finfl1
	2Tmax	2Fend
	3Ttot	1Finfl2
	1Finfl3	3Fend
	1Fend	Number of notes
	3Fmax	2Tmin
Régina	2Fmax	3Fend
	3Fmin	2Tmax
	Ttot	3Fbeg
	1Fend	1Finfl3
	3Fmax	2Ttot
	2Fbeg	
Village Saint Esprit	3Tmin	3Fbeg
	1Finfl1	1Finfl2
	2Tmax	3Tmax
	3Fend	2Fend
	1Tinfl1	1Ttot
	2Fmax	2Fbeg
	3Fmax	
Saint Georges	3Ttot	2Tmax
	3Tmin	1Ttot
	1Finfl3	2Fmin
	2Fmax	1Finfl2
	3Fend	2Fend
	2Ttot	1Fend
	3Fmax	2Fbeg

4. Discussion

We evidence here different dialectal patterns in short songs of both *C. cela* and *C. haemorrhous* males at different localities, and these dialects differed from year to year at all sites studied. However the differences between years in *C. haemorrhous*'s short songs are sometimes less contrasted than in *C. cela*'s, as far as we can directly compare these songs showing global similarities (short series of notes) but also structural differences between the two species (notably the detailed structure of end notes is more complex

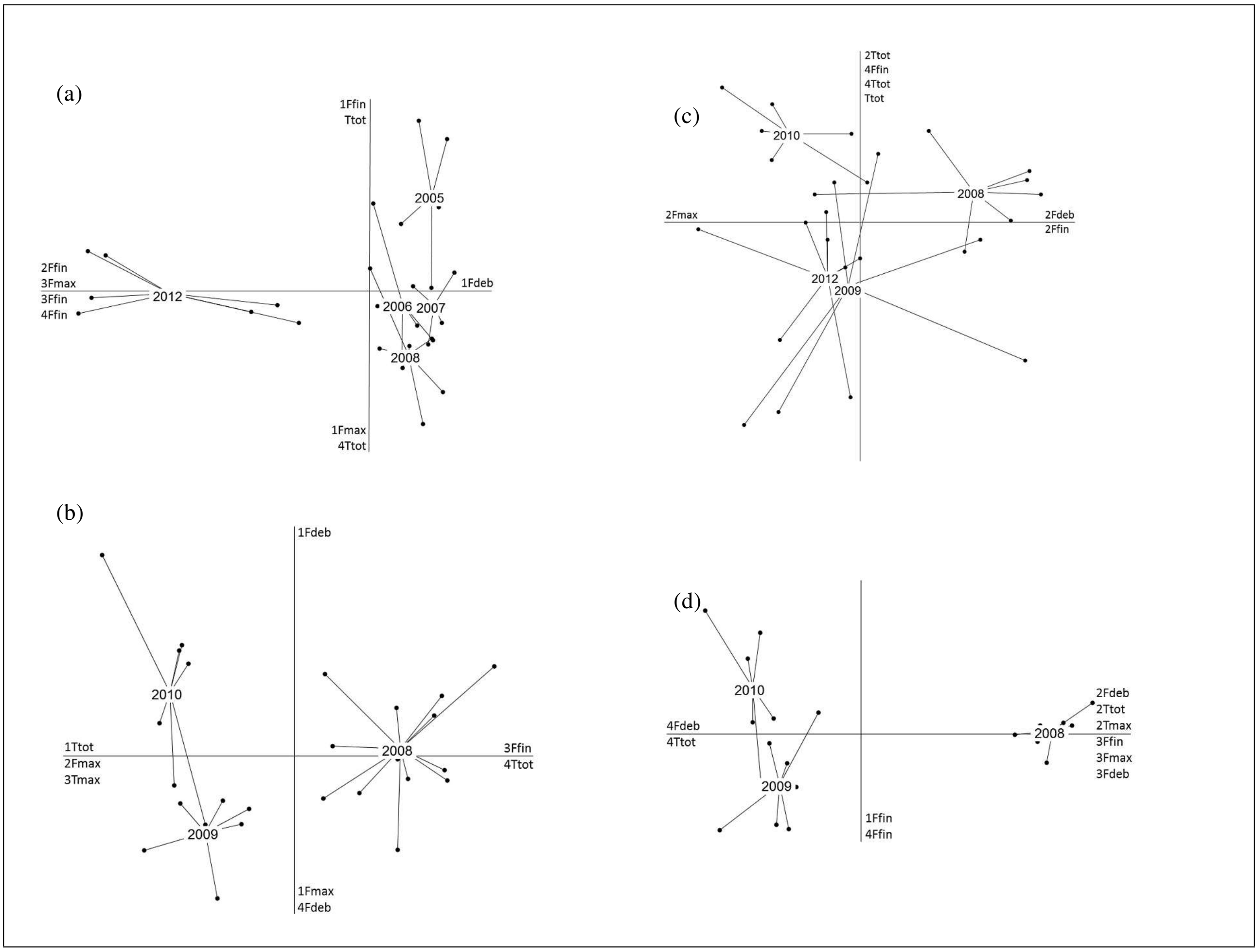

Figure 7. *C. haemorrhous* short songs. Two-dimensional PLS-DA graph of songs. Each point represents a short song. Abbreviations on X and Y axes = acoustic parameters with VIP>1 (determinant in the differences observed). Parameter abbreviations are preceded by the measured notes' numbers. Location a = Tonnégrande, b = Stoupan, c = Régina, d = Roura.

and variable in *C. cela*). But we never found exactly the same variants twice at any of the sites studied, so a more or less important annual variation seems to be the general rule in both species. The possible role of vocal plasticity versus social dynamics in the apparent lower amplitude of vocal variations in *C. haemorrhous* remains an open question.

As these birds were not banded we had no possibility to know whether the same individuals were recorded each year or whether other groups nested exactly at the same colony site. Although no information concerning dispersion is available (e.g. either juvenile dispersion or male versus female dispersal), these birds are known to usually return regularly to the same trees for breeding [29]. This faithfulness to nesting sites suggests a rather high stability of colonies across years and supports our suggestion that colonies as a whole do not typically migrate from a site to another, distant one.

The apparent differences in range of variations between the two species could be due to specific differences in vocal abilities. Notably, *C. haemorrhous*'s complete vocal repertoire is not as wide as *C. cela*'s. *C. cela*'s courtship song is more diversified and includes species mimicry and excellent imitations of diverse sounds of the environment. This species gives good imitation performances when emitting courtship songs, suggesting high vocal plasticity, and this ability is possibly expressed also by the relatively higher variability of their short songs.

At most of the localities studied, rapid changes were observed in the short song dialects of both species. These changes concern many acoustic parameters but not always the same ones, so environmental conditions or habitat cannot explain the changes in the acoustic structure, as would be the case if we observed a global uniform change in song frequencies or duration. We observed new song variants every year at the same period of the year and in the same context (breeding season), but changes could probably occur on a less than yearly basis (Feekes [29] observed progressive vocal drift over a period of only several months at *C. cela* nesting colony sites). Many songbird species present rapid changes (bobolinks [38], nightingales [39], village indigo birds [40], galahs [41]) attributed to cultural evolution and transfer rather than genetic drift. Hence differences may occur in the acoustic structure of specific song types, driven by copy inaccuracy, improvisation or rearrangement of existing song units [10, 12, 42]. Another

Table IV. *C. haemorrhous* acoustic parameters implied in differences between groups (years) (i.e. VIP>1) ranked by order of importance according to their VIP scores.

Matiti	3Tmax
	1Ttot
	2Ttot
	4Fbeg
	2Tmax
	Number of notes
	3Ttot
	2Fbeg
	4Fend
	1Fbeg
	1Fmax
Tonnégrande	1Fmax
	4Ttot
	2Fend
	3Fend
	1Fbeg
	3Fmax
	1Fend
	4Fend
	Ttot
Stoupan	3Fend
	2Fmax
	4Fbeg
	4Ttot
	1Ttot
	3Tmax
	1Fmax
	1Fbeg
Roura	2Fbeg
	3Fend
	4Fbeg
	4Fend
	1Fend
	2Ttot
	3Fmax
	4Ttot
	3Fbeg
	2Tmax
Régina	2Fend
	2Ttot
	4Ttot
	Ttot
	2Fbeg
	2Fmax
	4Fend
Village Saint-Esprit	Ttot
	3Fmax
	4Fend
	3Tmax
	2Tmax
	3Ttot

possibility is that rapid convergence could act as an affiliative signal. Scarl and Bradbury [41] demonstrated that galahs can change their call structures extremely rapidly (within 3 minutes) to match broadcast vocal stimuli. Convergence was observed during learning of contact calls by budgerigars [43]. This may be a way for birds to mediate interactions with individuals of different origins [41]. Both Cacicus species studied here gather at night in roosts and potentially interact with conspecifics from other colonies. One can therefore imagine that individuals from one particular colony have to adjust their short songs at colony sites quite regularly in order to maintain a group identity ("password", signature) in other contexts.

In the present study, we hypothesized that if yellow-rumped caciques' and red-rumped caciques' dialects have a social adaptation function, song dialects should change rapidly. Our results that demonstrate that changes occur at least on a year to year basis support the social adaptation hypothesis. We consider that our results do not support the "local adaptation" hypothesis predicting that females select males that produce local songs, because the short song is not a sexual song specially directed towards females during male courtship. Moreover, this hypothesis implies a long-term temporal stability of song structures as local songs are preferred to more divergent songs [5]. Our results suggest that these caciques probably learn their male short songs after dispersal and keep the capability to learn these social vocalisations well after reaching maturity and adjust to the continuous drift of colonial dialects.

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