Individual Variation of Whinnies Reflects Differences in Membership Between Spider Monkey (*Ateles geoffroyi*) Communities

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Abstract Contact calls, which function to coordinate group movement and maintain contact between conspecifics, are predicted to show high levels of acoustic variability and individual distinctiveness. We investigated interindividual variation in whinnies, a contact call, between two geographically distinct communities of wild Geoffroyi's spider monkeys (*Ateles geoffroyi*), which were experiencing different degrees of stability in membership due to immigration. We recorded whinnies from 18 subjects, including 9 females ranging within the Otoch Ma'ax Yetal Kooh Reserve, Punta Laguna, Mexico, and 9 females ranging within the Santa Rosa Sector, Area de Conservación Guanacaste, Costa Rica. We examined 13 acoustic parameters of female whinnies using principal component analysis and discriminant function analysis. Individual acoustic variability was significantly different between the two communities. A higher percentage of the whinnies of females were assigned to the correct caller in the community with only 3 individuals immigrating within 36 mo before and during data collection than in the community with 15 immigrant individuals during the same period. We suggest that the variation in interindividual distinctiveness for each community was influenced by the stability of the vocal environment, which was quantitatively different between communities because of changes in membership.

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Introduction

Individual recognition via vocalizations is important for effective communication, particularly when individuals are separated from visual contact (Spillmann *et al.* 2010), and it can occur in a variety of situations including parent–offspring interactions, kin recognition, mate-pair recognition, and intragroup interactions (Amorim and Vasconcelos 2008; Aubin and Jouventin 2002; Catchpole and Slater 2008; Mulard *et al.* 2008; Waser 1977). Individual recognition reflects a vocal identity or in-group membership when intraindividual variation of acoustic parameters is less than interindividual variation (Amorim and Vasconcelos 2008; Bee *et al.* 2001). The production of distinctive calls and their discrimination is expected whenever there is a positive tradeoff between the benefits and costs of being recognized (Wiley 1994). Individual distinctiveness in the acoustic features of calls has been documented in several species of nonhuman primates, including the pant-hoots of chimpanzees (*Pan troglodytes schwienfurthii*: Notman and Rendall 2005), long calls of male orangutans (*Pongo* spp.: Delgado 2007), loud calls of male baboons (*Papio cynocephalus ursinus*: Fischer *et al.* 2002), screams of juvenile vervets (*Cercopithecus aethiops*: Cheney and Seyfarth 1980), whinnies of spider monkeys (*Ateles geoffroyi*: Chapman and Weary 1990; Teixidor and Byrne 1997, 1999), lost calls and food calls of capuchins (*Cebus capucinus*: Digweed *et al.* 2007; Gros-Louis 2006), phee calls and long calls of Wied's marmosets (*Callithrix kuhlii*: Jorgensen and French 1998; Rukstalis *et al.* 2003), and phee calls of common marmosets (*C. jacchus*: Jones *et al.* 1993).

Of the multiple calls in a species vocal repertoire, contact calls function to coordinate community movement or to instigate and maintain contact between conspecifics (Kondo and Watanabe 2009; Marler 2004). Given that contact calls operate in intragroup social interactions, selection for individual distinctiveness is more likely in contact calls than in call types for which caller identification is not the primary function, e.g., alarm or intergroup loud calls (Bouchet *et al.* 2012). For example, of the previously mentioned call types that contain individually distinct cues, several are classified as contact calls, including chimpanzee pant-hoots (Notman and Rendall 2005), male orangutan long calls (Delgado 2007), spider monkey whinnies (Chapman and Weary 1990; Teixidor and Byrne 1997, 1999), capuchin lost calls (Digweed *et al.* 2007), and marmoset phee calls (Jones *et al.* 1993; Rukstalis *et al.* 2003). Although the basic categories of calls are thought to be innate and fixed, modification of the structure of existing calls is possible and enables a degree of vocal plasticity (Egnor and Hauser 2005; Fedurek and Slocombe 2011). For example, adult female Campbell's monkeys (*Cercopithecus campbelli*) produce a usually stable combined-harmonic contact call of which various acoustic features are individually specific. Some of these acoustic features change in response to changes in the community members' social interactions and may function to advertise recently established affiliative bonds between individuals (Lemasson and Hausberger 2004). The acoustic similarities of these calls are also better explained by the amount of time females spend grooming one another, rather than genetic similarities between females (Lemasson *et al.* 2011).

Vocal plasticity can occur when individuals are exposed to social learning opportunities in their acoustic environment, including the calls of conspecifics (Snowdon and Elowson 1999). Changes in community membership, as well as changes in affiliation between individuals, create significant social variability (Rukstalis *et al.* 2003) and affect opportunities for social learning to occur. Aspects of individuals' vocal communication that have a learned component are therefore likely affected by community membership changes as novel vocal elements are introduced into their acoustic environment and more familiar vocal elements cease to be practiced. Several species modify the acoustic structure of their calls as a result of changes to their social and therefore vocal environment, such as the arrival of immigrants, e.g., budgerigars (*Melopsittacus undulates*: Bartlett and Slater 1999), pygmy marmosets (*Cebuella pygmaea*: Snowdon *et al.* 1997), and acoustic contact with an unfamiliar group, e.g., budgerigars (Farabaugh *et al.* 1994), yellow-naped amazon parrots (*Amazona auropalliata*: Wright *et al.* 2008). Thus, a community experiencing greater stability in its membership, e.g., fewer immigrants, will exhibit a more stable vocal environment than a community experiencing lesser stability in its membership, e.g., more immigrants, as different vocal learning opportunities arise.

Individual vocal discrimination is particularly important for arboreal species as group members are often out of visual contact with one another (Ghazanfer and Santos 2004). For the same reason, it should be fundamental for species with a social organization characterized by a high degree of fission–fusion dynamics (Benson-Amram *et al.* 2011), where individuals from a stable community merge and separate over the course of hours, days, and weeks, resulting in subgroups of highly variable membership (Aureli *et al.* 2008). Spider monkeys (*Ateles* spp.) have such a social organization that requires consistent monitoring of subgroup membership for effective social interactions (Aureli and Schaffner 2008), and likely rely on individual vocal discrimination during intra- and intercommunity interactions (Ramos-Fernández 2005; *cf.* Crockford *et al.* 2004).

The vocal repertoire of Geoffroyi's spider monkey contains *ca*. 14 call types, and the "whinny" is the most common call produced (Chapman *et al.* 1989; Eisenberg 1976; Ramos-Fernández 2008). Whinnies are contact calls (Eisenberg 1976) that can carry for up to 300 m (Ramos- Fernández 2005) and often elicit a "whinny" response from one or more subgroup members (Ramos-Fernández 2008). The main function of whinnies is the maintenance of contact between community members (Eisenberg 1976; Ramos-Fernández 2005). Over larger distances, loud calls may be given to establish contact between highly dispersed subgroups (Spehar and Di Fiore 2013). Individual distinctiveness in whinnies has been already identified in previous studies of the same species (Chapman and Weary 1990; Ramos-Fernandez 2005; Teixidor and Byrne 1997, 1999). We investigated whether individual distinctiveness differs with the degree of stability in community membership by examining the nature of variation in the assignment of calls to the correct individual in two geographically distinct communities. We predicted that the community experiencing greater stability in its membership, i.e., fewer immigrants, and therefore a more stable vocal environment, would have a higher level of correct call assignment to individuals than the community experiencing lesser stability in its membership.

Methods

Ethical Note

Research was conducted at all times in accordance with the laws of participating countries. Permission to conduct research was granted by the University of Chester Psychology Department Ethics Committee, the Costa Rica Ministry of Environment and Energy (MINAE) permit no. ACG-PL-030-2006, and the Mexican government permit no. SGPA/DGVS/ 00910/13.

Study Sites and Subjects

We collected calls from individuals in two communities of wild Geoffroyi's spider monkeys (*Ateles geoffroyi*) that were identified using unique facial and body characteristics. One community ranged within the Otoch Ma'ax Yetel Kooh Reserve, Punta Laguna, Yucatan Peninsula, Mexico (hereafter the Punta Laguna community) (20°38′ N, 87°37′ W, 25 m elevation). The other community ranged within Santa Rosa Sector, Area de Conservación Guanacaste, Costa Rica (hereafter the Santa Rosa community) (10°50′ N, 85.37′ W, 25 m elevation). These two distinct geographic regions are phenologically similar, with seasonally dry tropical climates and a mosaic of primary and regenerating forests (Janzen 1986; Ramos-Fernández and Ayala-Orozco 2003). During the study period monthly rainfall totaled 2340 mm at Punta Laguna and 2648 mm at Santa Rosa (data courtesy of M. M. Chavarria Diaz, Santa Rosa and A. Alpuche Castillo, Comision National del Agua, Mexico). During the study period the Santa Rosa community consisted of 27–30 individuals, and the Punta Laguna community of 22–23 individuals (Table I). Before the study period the number of male and female adults and subadults that were resident for >36 mo was 10 (out of 25 adults and subadults = 40%) in the Santa Rosa community and 13 (out of 16 adults and subadults =81%) in the Punta Laguna community. During the 36 mo before the study period, 11 (44%) individuals immigrated into the Santa Rosa community and 2 (13%) immigrated into the Punta Laguna community. In addition, 4 (16%) individuals immigrated into Santa Rosa community and 1 (6%) immigrated into Punta Laguna community during the study period. Newly immigrant females were classified as those joining a community within the period of data collection. All other females from which calls were collected and analyzed had been resident in the community for ≥1 yr before recording calls commenced.

Data Collection

We collected data over an 18-mo study period, which incorporated wet and dry seasons at each site. In 2006 we collected data at Punta Laguna from January until mid-May and at Santa Rosa from mid-May through September. In 2007 we collected data at Santa Rosa from January until mid-May and at Punta Laguna from mid-May through September. Whinnies were recorded on an *ad libitum* basis from each community using a Sennheiser MKH shotgun microphone and a Marantz PMD 671 digital recorder. Visual identification of the caller and the context in which the monkey called had to be unambiguous for the call to be

Table I Composition of the two Geoffroyi's spider monkey study communities at Santa Rosa and Punta Laguna during 2006–2007

	2006			2007		
	Male	Female	Total	Male	Female	Total
Santa Rosa[a]						
Adult	6	9	15	6	8	14
Subadult	2	7	9	2	6	8
Juvenile	0	0	0	0	0	0
Infant	4	2	6	3	2	5
Total	12	18	30	11	16	27
Punta Laguna						
Adult	2	8	10	1	8	9
Subadult	1	0	1	3	3	6
Juvenile	2	2	4	2	2	4
Infant	5	2	7	4	0	4
Total	10	12	22	10	13	23

Adult = older than 8 yr; subadult = 5–8 yr; juveniles = 3–5 yr; infants 0–3 yr; individuals younger than 3 yr but whose mother had already another offspring were considered juveniles (Shimooka *et al.* 2008).

[a] Demographic data for age class classification were not available for adult and subadult individuals and so individuals were classified based on size. Subadults were individuals that moved independently from their mother, i.e., could be found in subgroups where the mother was not present, and were sexually mature, but were not fully adult size.

recorded. To reduce interference from background noise the distance between the caller and the microphone was kept to ≤15 m.

Acoustic Analysis

After sampling, we selected calls based on those with a high signal-to-noise ratio. Recordings were digitized using Avisoft SASLab Pro 4.40 (R. Sprecht, Berlin, Germany) with a sampling frequency of 44.1 kHz and 16 bits. We created spectrograms for each call using a 256-point fast-Fourier transform, flat top window function, bandwidth 648 Hz, and resolution 172 Hz. We measured 13 acoustic parameters from each spectrogram using the in-built program cursers (chosen based on Chapman and Weary 1990; Ramos-Fernández 2005; Teixidor and Byrne 1999; Catherine Crockford *pers. comm.*, October 31, 2006). Nine of these parameters were temporal measurements and the remaining four were frequency measurements (Fig. 1; Table II).

Statistical Analysis

We used a stepwise discriminant function analysis (DFA) to classify calls into predetermined, discrete categories, i.e., individual identities, based on their vocal structure. Before DFA we applied principal component analysis (PCA) to reduce the

Fig. 1 Spectrogram of Geoffroyi's spider monkey 'whinny' call showing examples of the 13 vocal parameters measured for analysis. Numbers in brackets refer to the corresponding numbers for each parameter in Table II.
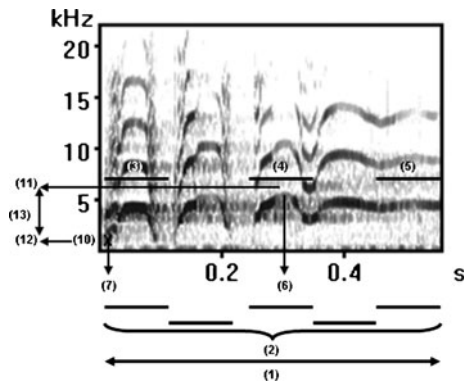
13 acoustic parameters to a smaller set of uncorrelated variables in order to minimize problems associated with multicollinearity and to ensure that the smallest sample group exceeded the number of predictor variables, and thereby protect from type I errors (Tabachnick and Fidell 2007). We used a varimax rotation and an eigenvalue >1.0 to determine the components that were extracted from the PCA (Tabachnick and Fidell 2007). All DFA tests were cross-validated

Table II Description of acoustic variables measured from spectrograms of whinnies of Geoffroyi's spider monkeys

	Acoustic parameter	Definition	Type of measure
1	Call duration[a,b]	Time from call onset to end of call (s)	Temporal
2	Modulation number[a,b]	Number of rising and falling oscillations of the fundamental	Temporal
3	Duration first modulation[a,b]	Duration of the first modulation (s)	Temporal
4	Duration middle modulation[a,b,c]	Duration of the middle modulation (s)	Temporal
5	Duration last modulation[a,b]	Duration of the last modulation (s)	Temporal
6	Location max. F0[a]	Location of the maximum fundamental frequency (s)	Temporal
7	Location min. F0[a]	Location of the minimum fundamental frequency (s)	Temporal
8	Rate of modulation production[a]	Rate of modulation production (no. of modulations/call duration)	Temporal
9	Location max. F0 as proportion[a]	Location of the maximum fundamental frequency as a proportion of the length of the modulation it occurs in (s)	Temporal
10	F0	Fundamental frequency (start frequency) (Hz)	Frequency
11	Max. F0[a,b]	Maximum fundamental frequency (Hz)	Frequency
12	Min. F0[a]	Minimum fundamental frequency (Hz)	Frequency
13	Frequency range[a]	Frequency range (Hz)	Frequency

[a] Call parameters used by Teixidor and Byrne (1997, 1999).

[b] Call parameters used by Chapman and Weary (1990).

[c] Middle modulation was measured as the earlier modulation when an even number occurred. For example, if six modulations were given, number 3 (not 4) was measured as the middle one. The number of each parameter refers to the correspondingly numbered parameter illustrated in Fig. 1.

using a leave-half-out procedure, creating the DFA model with half of the data set and then randomly testing it against the other half to test the classification power on a different set of calls than those on which the function was constructed. We set default levels used for entry criterion for the F value at 3.48 and removal was 2.71 (Tabachnick and Fidell 2007). We used χ^2 goodness-of-fit tests to determine if classification of call assignment differed from chance classification following the DFA. We used a paired t-test to examine the difference in correct classification of community individuals' calls when newly immigrant females were included and excluded. As the chance level differed owing to the inclusion and exclusion of newly immigrant females, we used the increase above chance level in correct cross-validated classification for each of the six remaining females to compare the two conditions. We used an unpaired t-test to determine whether correct call classification differed between communities. Statistical tests, except for the χ^2 tests, were performed using SPSS version 17.0.

Call Sample Sizes

Obtaining multiple, good quality calls from a large number of male monkeys was difficult as they travel more frequently at the boundaries of their home ranges than females (Chapman 1990) and were not encountered as often or for as long as females. For these reasons we analyzed only calls from females for this study. We collected a variable number of calls from each female. We excluded females with fewer than 10 viable calls from analysis. As our

Table III PCA rotated component matrix used for DFA for comparisons of individual Santa Rosa Geoffroyi's spider monkey whinnies during 2006–2007

Acoustic parameter[a]	Component				
	1	2	3	4	5
Call duration	**0.862**	0.211	0.001	−0.227	−0.072
Modulation number	**0.841**	−0.374	0.011	−0.199	−0.086
Location of min. F0	**0.771**	−0.042	0.044	−0.009	−0.076
Duration of middle modulation	**0.403**	0.357	−0.274	−0.135	0.245
Rate of modulation production	−0.018	**−0.938**	−0.015	0.025	−0.093
Duration of last modulation	−0.131	**0.907**	0.108	−0.002	−0.083
Duration of first modulation	0.323	**0.381**	−0.353	0.135	0.285
Relative position of max. F0	−0.171	0.006	**0.934**	0.007	0.069
Location of max. F0	0.292	0.105	**0.916**	−0.128	0.043
F0	−0.044	−0.042	−0.110	**0.874**	0.127
Min. F0	−0.311	0.034	0.005	**0.848**	−0.224
Frequency range	0.021	0.017	0.048	−0.382	**0.902**
Max. F0	−0.264	0.051	0.061	0.339	**0.850**

Bold figures represent the factors (left-hand column) that load most highly onto each component. Rotation method: Varimax with Kaiser normalization.

[a] See Table II for acoustic parameter definitions.

Table IV Summary of Wilks' lambda for the DFA of Santa Rosa Geoffroyi's spider monkey individuals' whinnies classification during 2006–2007

Test of function(s)	Wilks' lambda	χ^2	df	P
1 through 3	0.280	105.704	24	<0.001
2 through 3	0.564	47.574	14	<0.001
3	0.858	12.727	6	0.048

preliminary analysis on call parameters confirmed that there was no significant structural difference in the whinnies of adult and subadult females, individuals from these two age categories were analyzed together. These criteria provided viable calls from nine females from each community. For each female, we chose 10 calls randomly for analysis.

Results

Santa Rosa

Five components were extracted using PCA that together explained 80% of call variance between individual females. The temporal call parameters loaded highly on

Table V Classification of Santa Rosa Geoffroyi's spider monkey whinnies for individuals during 2006–2007, using DFA

	Subject code	Predicted individual classification									% whinnies correctly classified
		Esp	Bel	Ing	Gre	Sil	Gha	Syd	Hun	Mdg	
Original	Esp	1	4	1	1	1	0	0	0	2	10
	Bel	1	5	0	2	0	0	1	0	1	50
	Ing	4	0	2	0	1	0	3	0	0	20
	Gre	1	2	1	6	0	0	0	0	0	60
	Sil	0	0	2	0	2	1	0	5	0	20
	Gha	0	0	0	0	0	6	1	1	2	60
	Syd	0	0	3	0	0	3	3	1	0	30
	Hun	0	2	0	1	0	0	1	4	2	40
	Mdg	0	0	0	0	0	0	0	2	8	80
Cross-validated	Esp	0	4	2	1	1	0	0	0	2	0
	Bel	2	3	0	3	0	0	1	0	1	30
	Ing	4	0	2	0	1	0	3	0	0	20
	Gre	1	2	1	6	0	0	0	0	0	60
	Sil	0	0	3	0	1	1	0	5	0	10
	Gha	0	0	0	0	0	6	1	1	2	60
	Syd	0	0	4	0	0	3	1	1	1	10
	Hun	0	2	0	1	0	0	1	2	4	20
	Mdg	0	1	0	0	0	0	0	3	6	60

the first three components, whereas frequency parameters loaded highly on the remaining two components (Table III).

The DFA procedure resulted in three functions that accounted for 100% of call variation between Santa Rosa females. The first function explained 60% of variance, the second 30%, and the third 10%. All three of these functions contributed significantly to explaining call variation (Table IV). Of the 90 calls analyzed, 41% were assigned to the correct caller, which was significantly better than classification by chance, which was 11% (χ^2 test: $\chi^2 = 96.816$, df = 8, $P < 0.001$). With cross-validation 30% of calls were classified correctly, which was also significantly better than classification by chance (χ^2 test: $\chi^2 = 61.078$, df = 8, $P < 0.001$). Correct classification varied between 0 and 60% across individuals (Table V).

When analyses for the Santa Rosa community were re-run excluding the three newly immigrant females, classifications improved considerably. Using PCA five components were extracted that explained 81% of call variance (Table VI). Temporal parameters loaded highly on components 1, 2, and 4, whereas frequency parameters loaded highly on components 3 and 5.

DFA resulted in four functions that accounted for all call variance, with the first function explaining 52.4%, the second 32.1%, the third 13%, and the fourth 2.4%. The first three functions contributed significantly to call variance (Table VII). Of the 60 calls classified, 60% were assigned to the correct caller, which was significantly better than classification by chance, which was 16.7% (χ^2 test: $\chi^2 = 69.757$, df = 5, $P < 0.001$). These results held for the cross-validated procedure with 55% of calls correctly assigned

Table VI PCA rotated component matrix used for DFA for comparisons of individual Santa Rosa Geoffroyi's spider monkey whinnies excluding the new immigrants during 2006–2007

Acoustic parameter[a]	Component				
	1	2	3	4	5
Location of the min. F0	**0.813**	0.127	.074	0.192	–0.101
Call duration	**0.812**	0.156	–.397	–0.039	–0.036
Modulation number	**0.730**	–0.488	–.355	–0.016	–0.060
Duration of first modulation	**0.527**	0.229	.163	–0.248	0.217
Duration of middle modulation	**0.480**	0.279	–.045	–0.251	0.268
Rate of modulation production	–0.072	**–0.942**	.024	0.001	–0.114
Duration of last modulation	–0.008	**0.934**	.004	0.056	–0.112
Min. F0	–0.333	0.050	**.844**	0.012	–0.145
F0	0.124	–0.029	**.823**	–0.146	0.136
Relative position of max. F0	–0.275	–0.002	.061	**0.922**	0.012
Location of max. F0	0.255	0.079	–.222	**0.912**	–0.044
Max. F0	–0.122	0.019	.310	–0.012	**0.894**
Frequency range	0.186	–0.027	–.469	–0.019	**0.841**

Bold figures represent the factors (left-hand column) that load most highly onto each component. Rotation method: Varimax with Kaiser normalization.

[a] See Table II for acoustic parameter definitions.

Table VII Summary of Wilks' lambda for the DFA of Santa Rosa Geoffroyi's spider monkey individuals whinnies classification, excluding the three new immigrants during 2006–2007

Test of function(s)	Wilks' lambda	χ^2	df	P
1 through 4	0.180	92.627	20	<0.001
2 through 4	0.406	48.631	12	<0.001
3 through 4	0.719	17.794	6	0.007
4	0.943	3.177	2	0.204

(χ^2 test: χ^2 = 57.194, df = 5, P < 0.001). Correct classification varied between 40 and 70% for individuals (Table VIII). The increase above chance level in correct cross-validated classification of the six females was not significantly higher when newly immigrant females were excluded from the analysis procedure (55 ± 4.944) than when they were included (30 ± 7.993; paired t-test: $t(5)$ = 1.999, P = 0.102).

Punta Laguna

Five components were extracted in PCA, which together explained 80% of call variance between individual females. Temporal variables contributed heavily to the first three components, and frequency variables (with the exception of duration of first modulation) loaded highly on the fourth and fifth components (Table IX).

The DFA procedure resulted in five functions that explained 100% of call variance between individual females in the Punta Laguna community. The first function explained 35.1% of this variation, the second 27.5%, the third 23.8%, the fourth 11.3%, and the fifth 2.3%. The first four of these functions were significant (Table X). Of the

Table VIII Classification of Santa Rosa Geoffroyi's spider monkey whinnies during 2006–2007, using DFA excluding the three new immigrants

	Subject code	Predicted individual classification						% whinnies correctly classified
		Esp	Bel	Gha	Syd	Hun	Mdg	
Original	Esp	5	1	0	1	2	1	50
	Bel	2	6	1	0	0	1	60
	Gha	0	0	6	0	3	1	60
	Syd	1	0	2	7	0	0	70
	Hun	1	2	0	0	5	2	50
	Mdg	1	0	0	0	2	7	70
Cross-validated	Esp	4	2	0	1	2	1	40
	Bel	2	6	1	0	0	1	60
	Gha	0	0	6	0	3	1	50
	Syd	2	0	2	6	0	0	60
	Hun	1	2	1	0	4	2	40
	Mdg	1	0	0	0	2	7	70

Table IX PCA rotated component matrix used for DFA for comparisons of individual Punta Laguna Geoffroyi's spider monkey whinnies during 2006–2007

Acoustic parameter[a]	Component				
	1	2	3	4	5
Call duration	**0.949**	0.080	0.070	−0.103	0.021
Modulation number	**0.920**	−0.222	0.099	−0.139	−0.015
Location min. F0	**0.747**	−0.052	−0.157	0.081	−0.016
Rate of modulation production	−0.080	**−0.861**	0.026	−0.068	−0.124
Duration middle modulation	−0.056	**0.812**	−0.020	−0.172	0.105
Duration last modulation	−0.221	**0.761**	0.147	0.132	0.145
Location max. F0 as proportion	−0.263	0.049	**0.910**	−0.053	−0.014
Location max. F0	0.315	0.038	**0.893**	−0.193	−0.021
Min. F0	−0.197	−0.053	0.329	**0.818**	0.015
F0	0.093	−0.071	−0.349	**0.715**	0.166
Duration first modulation	−0.036	0.096	−0.255	**0.637**	0.048
Frequency range	0.048	0.227	−0.116	−0.082	**0.955**
Max. F0	−0.074	0.173	0.092	0.416	**0.869**

Bold figures represent the factors (left-hand column) that load most highly onto each component. Rotation method: Varimax with Kaiser normalization.

[a] See Table II for acoustic parameter definitions.

90 calls analyzed, correct classification was considerably higher than for the Santa Rosa community, with 64.4% of calls assigned to the correct caller. This classification was significantly better than classification by chance, which was 11% (χ^2 test: $\chi^2 = 229.406$, df = 8, $P < 0.001$). Cross-validated results classified 57.8% of calls correctly, which was also significantly better than classification by chance (χ^2 test: $\chi^2 = 180.75$, df = 8, $P < 0.001$). Correct classification varied between 30 and 100% for individuals (20–80% cross-validated) (Table XI). Excluding the only newly immigrant from the analyses did not affect results for Punta Laguna females, with cross-validated classification 57.5%.

When we compared the cross-validated classification levels between the two communities we found a significant difference in individual classification between the nine Santa Rosa females and the nine Punta Laguna females (unpaired t-test: $t(16) = 2.64$, $P = 0.018$; Fig. 2), indicating that the individual calls of Punta Laguna females were assigned to the correct caller significantly more often than the individual calls of Santa Rosa females.

Table X Summary of Wilks' lambda for the DFA of Punta Laguna Geoffroyi's spider monkeys individuals whinnies classification during 2006–2007

Test of function(s)	Wilks' lambda	χ^2	df	P
1 through 5	0.065	223.562	40	<0.001
2 through 5	0.156	152.207	28	<0.001
3 through 5	0.327	91.780	18	<0.001
4 through 5	0.633	37.437	10	<0.001
5	0.917	7.090	4	0.131

Table XI Classification of Punta Laguna Geoffroyi's spider monkey whinnies for individuals during 2006–2007, using DFA

	Subject code	Predicted individual classification									% whinnies correctly classified
		Ame	Cec	Chi	Cla	Flo	Hel	Joa	Lol	Ver	
Original	Ame	6	0	0	0	0	0	2	0	2	60
	Cec	0	8	0	0	0	1	0	0	1	80
	Chi	1	0	7	1	0	0	0	0	1	70
	Cla	0	0	0	10	0	0	0	0	0	100
	Flo	0	2	0	2	4	0	1	1	0	40
	Hel	0	0	0	0	2	7	0	0	1	70
	Joa	2	0	1	0	2	1	3	1	0	30
	Lol	1	0	0	0	0	0	3	6	0	60
	Ver	2	0	1	0	0	0	0	0	7	70
Cross-validated	Ame	6	0	0	0	0	0	2	0	2	60
	Cec	0	8	0	0	0	1	0	0	1	80
	Chi	1	0	6	1	1	0	0	0	1	60
	Cla	0	0	1	8	0	0	1	0	0	80
	Flo	0	2	1	2	2	0	2	1	0	20
	Hel	0	0	0	0	2	6	0	1	1	60
	Joa	2	0	1	0	2	1	3	1	0	30
	Lol	1	0	0	0	0	0	3	6	0	60
	Ver	2	0	1	0	0	0	0	0	7	70
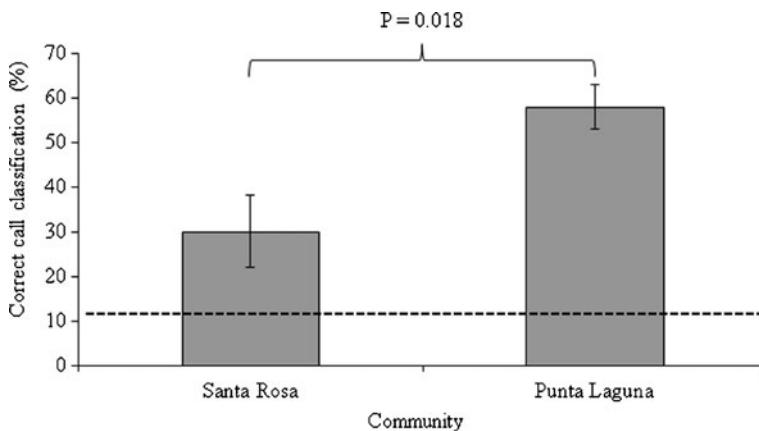
Fig. 2 Mean (±SE) cross-validated correct call classification of the two Geoffroyi's spider monkey study communities at Santa Rosa and Punta Laguna during 2006–2007. The hash line indicates a chance classification rate (11%). There is a significant difference in intragroup individual call classification between the two communities (unpaired t-test: $t(16) = 2.64$, $P = 0.018$).

Discussion

As in previous studies examining whinnies of Geoffroyi's spider monkeys, we found evidence that calls contain information about the identity of the caller (Ramos-Fernández 2008). Our acoustic analysis provides evidence that variation in correct call assignment may be related to the stability in community membership. Although in each community females' calls were assigned to the correct caller significantly better than chance, the two communities showed different levels of correct call assignment. Significantly more calls were assigned to the correct caller in the Punta Laguna community than in the Santa Rosa community, which experienced more changes in membership. Within the Santa Rosa community, classification to the correct caller was higher when immigrants were removed from the analysis than when they were included, but not significantly higher, a result that could have been due to small sample size ($N = 6$). Further, the PCA conducted on each community identified different underlying components to describe the variance between females' calls (Tables III and IX). Our PCA results suggest that variance between females' calls within the same community was not dominated by one specific call characteristic, e.g. differences in call duration or differences in frequency range, but was accounted for by individual variation in the use of several call parameters. This finding is consistent with many studies showing that significant variation in animals' calls lies in multiple acoustic parameters (Ehret 1990; Fischer et al. 2001; Hammerschmidt and Todt 1995; Owren et al. 1992).

Various factors might account for the differences we observed across the two sites other than the degree of stability in community membership. It is possible that some variation in the acoustic structure of females' calls from the two communities was due to habitat differences affecting call transmission of recordings (Brown and Gomez 1992). However, this is unlikely as all recordings took place in areas with little undergrowth, resulting in a clear visual path between the recorder and caller, and the distance between the recorder and caller was never >15 m. The possibility that body size differences in females between sites accounted for the variation (Fitch 1997; Fischer et al. 2002) is also unlikely, as no discernible size differences were observed and no such differences have been reported for Geoffroyi's spider monkey (Ford and Davis 1992). The degree of genetic relatedness among the analyzed females in each community was low, except for a single mother–daughter dyad in the Punta Laguna community (F. Aureli, A. Di Fiore, and C. Schaffner unpubl. data), and there were no errors in the classification of whinnies between them. That the majority of females were not first-, second-, or even third-degree relatives suggests genetics do not play a large role in successful whinny classification in our study. Given the likely negligible impact of the above three factors, stability in community membership, i.e., the relative number of new immigrants in the community, remains an important factor that may account for the variation in successful call assignment across sites.

Residency duration was very different between the two communities: 81% of adult and subadult individuals resided in the Punta Laguna community for >3 yr before the study, whereas only 40% of individuals did so in the Santa Rosa community. In addition to the four females who joined the Santa Rosa community during the data collection period, in the 5 mo before data collection five males joined the community and the long-term resident males disappeared along with other adult and juvenile community members (Aureli et al. 2013). This is not typical for spider monkey

communities (Shimooka *et al.* 2008). Thus, stability of membership was different between the two communities, a factor known to affect levels of affiliation among spider monkeys and overall community cohesion in captive settings (Pastor-Nieto 2001).

Changes in community membership likely affected the vocal environment of the Santa Rosa community, as the relatively high number of recent immigrant individuals, likely coming from different communities, probably introduced a number of novel call elements, resulting in an influx of unfamiliar acoustic cues. In previous studies, monkeys appear to share more vocal characteristics as a means to establish or strengthen new social relationships. For example, in female Campbell's monkeys the sharing of vocal variants between individuals was suggested to occur more often in socially disturbed groups than in stable groups, as a way of advertising the formation of novel affiliative bonds to other group members (Lemasson and Hausberger 2004). Pygmy marmosets also modify characteristics of their trill calls after pairing with an unfamiliar individual, including duration, peak frequency, and modulation rate (Snowdon and Elowson 1999). Thus, the presence of more recent immigrants in the Santa Rosa community might have resulted in a greater intraindividual variation in call structure.

As there is evidence for community-specific parameters in Geoffroyi's spider monkey whinnies (Santorelli, C., Aureli, F., Ramos-Fernández, G. & Schaffner, C. unpubl. data), the lower level of call assignment to the correct individual in the Santa Rosa community may capture a transitional acoustic phase as individuals adjust to changes in community membership. Call convergence, i.e., when novel acoustic features are incorporated into an existing repertoire, also results in individually distinct acoustic features being reduced (Candiotti *et al.* 2012), and may be the process through which this transitional acoustic phase occurs. Further, like unfamiliar male budgerigars forming new "cage"-specific calls when housed together (Farabaugh *et al.* 1994) and pygmy marmosets sharing elements of their trill vocalization when newly paired (Snowdon and Elowson 1999), the ability to adjust call structure in the face of changing community membership may not be restricted to new immigrants. Indeed, our study indicated that poor classification also included females that belonged to the community for several years at both sites. In Punta Laguna the lowest correct classification level belonged to a female, which was in the community as an adult in 1997, and a female that joined the community 17 mo before data collection. In Santa Rosa they were from a new immigrant, a female that had been an established adult in the community at least since 2003, and a female that was a juvenile in the community in 2003 and a subadult by the time data collection began. This pattern of findings has two potential implications: Successful individual call classification is not always associated with how long a female has resided in a community, as females that belonged to a community for several years did not necessarily have a more distinctive call structure than newer immigrants, and both new and longer term residents may also change elements of their call structure when exposed to new call variants.

There is also variation in the extent of correct call assignment across studies conducted on the same Santa Rosa community. In our study correct call classification was 30%, whereas it was 44% in Chapman and Weary (1990) and 72% in Teixidor and Byrne (1999). In addition to possible differences in membership stability, differences in methodological procedures between our study and the two previous studies may have contributed to the discrepancy between correct assignment levels. We collected calls from a closer distance (≤15m) than Chapman and Weary (1990), which may have

increased the background noise they recorded, reducing the fine details of auditory signals. Additional temporal and frequency parameters were also measured in our study. Further, we applied PCA to the data before DFA, whereas neither earlier study did so. The earlier studies also used smaller sample sizes for analysis and included individuals from different age cohorts, and individual variation was likely heightened by variation due to age differences (*cf.* Fischer 2002). Finally, although the three studies focused on the same community, it is highly likely that monkey subjects were different in each study, as there was nearly a decade between the two closest data collection periods.

Our analyses confirm that individual distinctiveness is a feature of whinnies, and demonstrate its variability between communities, particularly when there is high turnover in community membership. Our findings suggest that vocal learning, when an individual modifies the acoustic structure of a vocalization as a result of experience (Janik and Slater 2000), is an ongoing process in Geoffroyi's spider monkeys, as it occurs in adulthood and is strongly supported by the possibility that both new and longer term residents may change elements of their call structure when exposed to new call variants. Investigating the influence of call convergence as a possible mechanism underlying this learning processes would be an intriguing possibility for future research. Overall, our study provides an important and novel contribution to the understanding of how changes in the vocal environment, such as those due to immigrant individuals, can lead to novel acoustic features being incorporated into a current repertoire.

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