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ORIGINAL ARTICLE

Age and social affinity effects on contact call interactions in free-ranging spider monkeys

M. Briseno-Jaramillo[1] · **G. Ramos-Fernández**[2,3] · **T. M. Palacios-Romo**[1] · **J. R. Sosa-López**[1] · **A. Lemasson**[4]

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Abstract

Nonhuman primates' vocal repertoire has shown little plasticity, with immatures producing adult-like acoustic structures. Yet, the use of different call types shows a degree of socially dependent flexibility during development. In several nonhuman primate species, group members exchange contact calls respecting a set of social and temporal rules that may be learned (e.g., overlap avoidance, turn-taking, social selection of interacting partners, and call type matching). Here, we study the use of contact calls in free-living adult and immature (old and young) spider monkeys (*Ateles geoffroyi*). We focused our study in two contact call types of the species' repertoire: whinnies and high-whinnies. Our results suggest that individuals in all age classes produced both call types, with immatures producing less frequently the whinny call type. Immature individuals exchanged calls less often than adults, although their contribution increased with age. Conversely, mature individuals regulated their emissions by (1) exchanging more calls with their preferred affiliative partner and (2) matching the call type, while immatures did not. Our results show that contact call usage changes during development and suggest that adult rules might be learned. We argue that call matching is a "conversational rule" that young individuals acquire with apparent call-type-dependent variations during development. Our findings support the idea that social factors influence vocal development in nonhuman primates.

Significance statement

We studied the social rules underlying vocal interaction patterns in free-ranging spider monkeys. We found that, while both immature (old and young) and mature individuals were able to produce the two species contact call types, they differed strongly in the way they used them. Matures called more often and exchanged more, while the vocal response rates of immature individuals increased with age. Also, mature individuals exchanged preferentially with their close associates and matched their call types while immatures did not. As in other species, we predict that these exchange patterns serve as a social rule to maintain and strengthen social bonds between individuals. We discuss our findings in light of the probable role of social learning during acquisition of the appropriate context of calling and of the response to others' calls. These findings support the idea that social influences guide vocal development in nonhuman primates.

Keywords Acoustic matching · Call exchanges · New World monkeys · Vocal communication · Vocal learning

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J. R. Sosa-López and A. Lemasson contributed equally to this work.

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✉ M. Briseno-Jaramillo
mar.briseno.jaramillo@gmail.com

[1] CONACYT-Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Oaxaca (CIIDIR), Instituto Politécnico Nacional, Oaxaca, Mexico

[2] Instituto de Investigaciones en Matemáticas Aplicadas y en Sistemas, Universidad Nacional Autónoma de México, Mexico City, Mexico

[3] Unidad Profesional Interdisciplinaria en Ingeniería y Tecnologías Avanzadas, Instituto Politécnico Nacional, Mexico City, Mexico

[4] Univ Rennes, Ethologie Animale et Humaine, Paimpont, U.M.R. 6552 - C.N.R.S - Université Caen Normandie, Paimpont, France

Introduction

Historically, vocal learning in a social context has been considered as an ability limited to a small group of species (songbirds, Farabaugh et al. 1994; cetaceans, Tyack and Sayigh 1997; bats, Boughman 1998; elephants, Poole et al. 2005; humans, Goldstein and Schwade 2008). Recent discoveries, however, have shown that vocal learning under social influences is possible in a broader range of species (e.g., *Mus musculus*, Arriaga et al. 2012; *Capra aegagrus hircus*, Briefer and McElligott 2012; *Gazella subgutturosa*, Volodin et al. 2013), including nonhuman primates (review in Bouchet et al. 2013). Whether vocal behaviors are socially learned or inherited in nonhuman primates has been subject to intense debate (Hammerschmidt and Fischer 2008; Lemasson et al. 2013a). The evidence shows that the social experience during the development of vocal behaviour strongly affects call usage (i.e., call rate and context of emission of the call) and perception (i.e., discrimination of acoustic variations and comprehension of the call function), but also, to a lesser extent, call production (i.e., acoustic structure of the call) (Janik and Slater 1997; Seyfarth and Cheney 1997; Boughman and Moss 2003; Lemasson et al. 2011a).

Nonhuman primates present a strong innate predisposition in the perception and production of species-specific vocalizations. For example, concerning perception, newborn chimpanzees (*Pan troglodytes*) show cardiac accelerations when exposed to conspecific but not to heterospecific alarm calls (Geary 2003). Young squirrel monkeys (*Saimiri sciureus*) reared with surrogate mothers (object covered with cotton fabrics which contained a loudspeaker) responded appropriately at acoustic stimuli, i.e., decreasing vs increasing contact when respectively exposed to agonistic vs contact calls (Herzog and Hopf 1984). On the production side, studies have shown that even monkeys deprived from social (e.g., squirrel monkey; Winter et al. 1973; Lieblich et al. 1980; Hammerschmidt et al. 2001) and auditory (e.g., squirrel monkey, Talmage-Riggs et al. 1972) experiences during their early life, eventually producing adult-like acoustic structures (review in Hammerschmidt and Fischer 2008). Cross-fostering experiments (rhesus macaques, *Macaca mulatta*, Owren et al. 1992) and acoustic analyses of hybrid offspring vocalizations (capped gibbon, *Hylobates pileatus*, and common gibbon, *H. lar*, Geissmann 1984) confirmed a strong influence of genetics on vocal behaviour. Nonetheless, a few other studies suggest that innate factors do not explain all the acoustic variability observed after birth (social deprivation, Newman and Symmes 1974; hybridization, Hodun et al. 1981; Masataka and Symmes 1986; cross-fostering, Masataka and Fujita 1989; deafening, Roupe et al. 2003) suggesting that there are other factors such as social experience (e.g., vocal copying) and morphological changes throughout development (maturation) involved.

Among non-socially driven factors, changes in morphological structures related with sound production during development could explain some of the variation observed in acoustic signals. Some of the differences in the fine structural characteristics of vocalizations are the consequence of developmental changes in the vocal tract anatomy (squirrel monkeys, Lieblich et al. 1980; vervet monkey, *Cercopithecus aethiops*, Hauser 1989; pig-tailed macaque, *Macaca nemestrina*, Gouzoules and Gouzoules 1989; pygmy marmoset, *Cebuella Pygmaea*, Elowson et al. 1992). Change in lung or larynx sizes, and hormonal profiles, may influence call durations and frequencies, resulting in age- and sex-related acoustic differences (Gautier and Gautier 1977; Ey et al. 2007).

During the last decade, a growing number of studies on various taxa of primates have shown some degree of acoustic variation in adult calls, where the acoustic structure of a given call type is not fixed and can be refined to some extent, suggesting vocal plasticity (Snowdon and Elowson 1999; Lemasson et al. 2011a; Watson et al. 2015). The studies available suggest acoustic convergences among specific affiliates within a group (gibbons, Geissmann 1999; marmosets, Snowdon and Elowson 1999; Campbell's monkeys, *Cercopithecus campbelli*, Lemasson et al. 2011a; chimpanzees, Watson et al. 2015; Japanese macaques, Lemasson et al. 2016) or, at a broader scale, within a specific population (e.g., lemurs, *Microcebus murinus*, Hafen et al. 1998; chimpanzees, Mitani et al. 1999; Crockford et al. 2004; Braune et al. 2005, macaques, *Macaca fuscata*, Tanaka et al. 2006; pygmy marmosets, de la Torre and Snowdon 2009). Several of these studies confirmed that social factors, and not genetic drift or habitat quality, explain the observed acoustic variation, but only a few of them conducted long-term surveys and observed acoustic changes over time (Elowson and Snowdon 1994; Lemasson and Hausberger 2004). In addition, some cases of vocal innovation in captive populations have been suggested by several authors (i.e., emergence of entirely new call types; chimpanzees, Hopkins et al. 2007; Campbell's monkeys, Ouattara et al. 2009a; orangutans, Lameira et al. 2016).

Studies on juvenile primates have also demonstrated plasticity during the development of vocal behaviors. For example, acoustic analyses in marmosets (*Callithrix jacchus*) showed that infant and juvenile vocalizations changed progressively toward the vocalizations produced by adults (Pistorio et al. 2006). Infant marmosets (Elowson et al. 1998) and tamarins (Snowdon 2009) produce long series of repeated vocalizations, some being clearly adult-like and other being unique (absent from the adult repertoire), a phenomenon that can be compared with human babbling. As young marmosets mature, they show a decrease in bout length and an increase in the proportion of adult-like calls (Snowdon and Elowson 2001). Auditory feedback and social interactions, notably with parents, influence the refinement of call production and usage, facilitating learning of immatures (Takahashi et al. 2015). Female gibbons (*Hylobates agilis*) also produce songs that become more acoustically similar and more synchronous with those of their mother along development (Koda et al. 2013).

In addition to call production, evidence for social learning in juveniles is supported by studies on call usage and perception (review by Seyfarth and Cheney 1997; Snowdon 1997 and Bouchet et al. 2013), as previously mentioned. For example, a gradual development and learning of the function of calls have been reported in several species. Young monkeys learn the appropriate contexts in which calls have to be emitted and how to respond appropriately (e.g., vervet monkeys, *Chlorocebus pygerythrus*, Cheney and Seyfarth 1992; macaques, *Macaca nemestrina*, Gouzoules and Gouzoules 1989). The same is true for the appropriate usage of (and response to) greeting calls by young chimpanzees (Laporte and Zuberbühler 2011) and Japanese macaques (*Macaca fuscata)* (Katsu et al. 2014). In cotton top tamarins (*Saguinus oedipus*), juveniles learn the appropriate usage and meaning of food calls (Roush and Snowdon 1994, 2001).

More recently, some research has focused on vocal exchanges. This is a particular form of calling behaviour that involves at least two individuals, which respond to each other within a brief time lapse (Bouchet et al. 2017). Most of these studies conducted temporal analysis of calling patterns in order to confirm that the recorded calls formed part of a coordinated vocal exchange, and thus differ from spontaneous calling events such as isolated calls or choruses (e.g., Sugiura and Masataka 1995; Mendes and Ades 2004; Lemasson et al. 2010, 2018). Interestingly, this behaviour involves combined skills in call production, usage, and perception. Vocal exchanges follow specific social rules such as the threshold of vocal response delay, avoiding call overlap, turn-taking between interacting partners and selection of preferred interacting partners (Snowdon and Cleveland 1984; Sugiura and Masataka 1995; Lemasson et al. 2010, 2011b; Takahashi et al. 2013). Within vocal exchange, vocal matching is one of the most notorious behaviors, where an individual responds to the interacting partner with the same call type (Japanese macaques, Sugiura and Masataka 1995; chimpanzees, Mitani and Gros-Louis 1998; Diana monkeys, Candiotti et al. 2012; gibbons, Koda et al. 2013). The few available studies have shown that some of these vocal exchange rules may be socially learned (Lemasson et al. 2011b, 2013a; Chow et al. 2015; Bouchet et al. 2017). Some of these studies showed that juveniles break the conversational rule much more often than adults and, conversely to adults, do not respond differently to playbacks of vocal exchanges respecting or not the conversational rule (turn-taking—Lemasson et al. 2011b, call matching—Bouchet et al. 2017).

Spider monkeys maintain specific social relationships keeping long-term affiliative bonds (Ramos-Fernández 2008), reflected by high grooming rates (Aureli and Schaffner 2008), so we can predict that affiliates are also preferred partners of contact call exchanges. However, little is known about contact call development (Eisenberg 1976; Ramos-Fernández 2005; Vick 2008). Three-month-old individuals produce the two contact call types of the species (Eisenberg 1976). These two calls are the most frequently emitted in the repertoire of our study species: whinny (Eisenberg 1976; Chapman and Weary 1990; Teixidor and Byrne 1999; Ramos-Fernández 2005) and high-whinny (Ramos-Fernández 2005, equivalent to the “trill” by Eisenberg 1976). There is also evidence that these calls contain information about the individual identity of the caller (Teixidor and Byrne 1999; Ramos-Fernández 2005), which is decisive for our study. However, nothing is known about the temporal and social patterns of contact call exchanges in adults and in unexperienced individuals.

It is considered challenging to communicate in habitats with limited visibility (i.e., dense forest) and in social groups with a high degree of fission-fusion dynamics (i.e., where individuals spend long periods of time apart from each other, Aureli et al. 2008). The use of acoustic signals for interacting with other members is expected to be essential in spider monkeys (*Ateles geoffroyi*), making possible to stay in contact with specific partners even at distance (Ramos-Fernández 2005). Spider monkeys maintain specific social relationships keeping long-term affiliative bonds (Ramos-Fernández 2008), reflected by high grooming rates (Aureli and Schaffner 2008). However, little is known about vocal development (Eisenberg 1976; Ramos-Fernández 2005; Vick 2008). Three-month-old individuals are able to produce the two contact call types of the species (whinny and high-whinny) (Eisenberg 1976).

Inherited factors could determine the general species-specific call repertoire, while social factors could influence the use of call types. The role of social experience in the use of species-specific vocalizations has been reported for several species of nonhuman primates (Japanese macaques, Masataka 1985; vervet monkeys, Seyfarth and Cheney 1986; pigtail macaques, Gouzoules and Gouzoules 1989). Studies in squirrel monkeys showed that infants gradually develop the ability to recognize and respond to the contact calls of individuals within their social groups (McCowan and Newman 2000). Social affinity is determinant for vocal learning (Lemasson et al. 2011a). In chimpanzees, the acquisition of pant-grunting behaviour (greeting’ signal accompanied by a pant-grunt call) is a long-lasting process in which social influences by the mother and other group members are likely to play a role (Laporte and Zuberbühler 2011). In spider monkeys, we know that during the time in which immatures are dependent, their mothers primarily determine their associations with other group members (Vick 2008). However, it is during this period that immatures develop social relationships with other group members.

Through their interactions with other group members in a dynamic grouping pattern such as fission-fusion dynamics, they progressively develop their appropriate adult social roles (e.g., Vick 2008). However, how socialization co-develops with contact call usage remains an open question as well.

In this study, we evaluated whether spider monkeys use the two contact calls (whinnies and high whinnies) in a similarly way at different ages and whether social affinity influences their vocal behaviour. If vocal usage in spider monkeys is learned, we expected contact calls to be involved in affiliative vocal exchanges with opportunity for socially guided vocal development. We evaluated the influence of callers' characteristics on vocal behaviour. Particularly, we explored whether age has an effect on (1) call rate and (2) individual response rate, and whether the effect is similar for both call types. We also assessed the influence of caller's age on the vocal response patterns. Particularly, we tested whether (3) a higher social affinity is associated to higher exchange rates, and then (4) whether matching behaviour occurs more often than non-matching events depending on call type and caller age.

Methods

Study site and subjects

The study site is located within the *Otoch Ma'ax Yetel Kooh* reserve, close to Punta Laguna village (Yucatan Peninsula, Mexico—20°38′ N, 87°38′ W). The habitat consists of a mosaic of vegetation that includes a 60-ha fragment of semi-evergreen medium forest (with trees up to 25 m height) and an area of forest in different stages of secondary succession (with trees less than 15 m height; Ramos-Fernández and Ayala-Orozco 2003).

Field work was conducted from September 2016 to April 2017. During this period, 98 days in total, one observer (MBJ) collected all the data on a single group of free-ranging black-handed spider monkeys (*Ateles geoffroyi*) composed of 40 individuals (14 mature females, 6 mature males, 12 immature females and 8 immature males). Three experienced field assistants occasionally helped with the tracking and identification of the individuals. This group has been studied continuously for the past two decades and is thus fully habituated to human observers (Aureli et al. 2008; Slater et al. 2009; Ramos-Fernández et al. 2018). Identities of all members and their ages (if born in the group) are known (Table 1). In this species, the majority of the females emigrate from their natal group around the time of reproductive maturity, but this is much less constant in males (Symington 1987), therefore, most maternal filiations are also known (see Table 1). Identification of each individual was done in the field based on facial markings, pelage coloration and distinguishing marks on the genitalia. In this species, individuals reach sexual maturity around the age of 5 years old (Symington 1987), when females usually emigrate from their natal group (Vick 2008). At this stage, adults become sexually active even if they reach a full adult size around 8 years old (Shimooka et al. 2008). Thus, in this study we categorize individuals as mature from 5 years on.

Behavioral observations and vocal recordings

Groups of spider monkeys have a high degree of fission-fusion dynamics, with the total group splitting into smaller subgroups that constantly vary in size, cohesion, and composition (Aureli et al. 2008). All individuals positioned not more than 30 m from one another at a given time are considered members of a given subgroup. Ramos-Fernández (2005) established this criterion choosing one focal adult individual and measuring the distance between this monkey and all other individuals within a 200-m radius. He repeated the procedure five times on different days, with different focal individuals and generated a graph showing the number of individuals at different distances. Posteriorly, he selected a cutoff of 30 m as the shortest distance at which the graph showed a steep decline.

Observations were conducted on all possible individuals, i.e., 20 matures and 16 immatures (Table 1). It was not possible to record data blind because our study involved focal animals in the field. Immatures were 3.0 ± 1.3 (mean ± standard deviation) years old at the mid-time of the study period. We divided immatures into two categories, old immature ($N = 8$) from 4 to 5 years old and young immature ($N = 8$) from 1 to 3 years old, since individuals of 4 years old are more likely to leave natal group (Symington 1987). Four youngsters (all being less than 1 year old) had to be discarded from the analysis since they were never recorded emitting the contact call types included in this study. Several subgroups were followed during consecutive days (observations were done 2 days 4 h and 3 days 8 h per week) during a total of 548 h. Because the size and the composition of these subgroups can be widely variable (mean ± standard deviation of subgroup size: 8.1 ± 5.0 individuals), the observed subgroup was semi-randomly selected trying to equalize the total number of observation hours per individual (mean and standard deviation were 83.7 ± 15 h per individual, see Table 1). To do so, the observer followed different types of subgroups on consecutive days and switched subgroups which composition did not change after 3 h in a given day. Therefore, the time spent with a given subgroup varied (mean ± standard deviation: 3hrs16min ± 1hr38min).

We recorded all the data (grooming interactions and call emissions) using the *all occurrence sampling* method, that records all instances of a given behaviour performed by any individual in the subgroup during a given time period (Altmann 1974). We selected this sampling method because a subgroup size is relatively small, grooming is not a frequent

Table 1 Group composition and individual characteristics of spider monkeys (*Ateles geoffroyi*) in the Otoch Ma'ax Yetel Kooh reserve, Yucatan Peninsula, Mexico

Individual code	Sex	Mother identity	Age	Birthday	Immigration year[a]	Total observation (h)
CH	F	?	MA		1996	106.5
MS	M	CH	MA	15/07/2007		80.5
KO	M	CH	MA	06/04/2010		64.5
LO	F	CH	MA	11/11/2001		100.8
VA	F	LO	MA	11/12/2009		93.3
FL	F	?	MA		1996	73.8
JN	M	FL	MA	01/12/2003		88.4
VE	F	?	MA		1996	103.6
EG	M	VE	MA	16/01/2004		92.4
KL	F	?	MA		2002	59.5
JA	F	?	MA		2004	89.5
WB	M	JA	MA	11/12/2010		59.1
HI	F	?	MA		2010	84.7
PC	F	?	MA		2011	81.6
TG	F	?	MA		2011	76.7
ML	F	?	MA		2013	87.6
AE	F	?	MA		2013	71.6
MI	F	?	MA		2015	58.4
EL	F	?	MA		2014	65.2
TL	M	CL	MA		2001	87.9
TK	F	CH	OI	10/12/2012		96.5
NA	M	CH	YI	29/01/2015		106.5
LE	F	LO	OI	09/11/2012		100.8
ES	F	LO	YI	01/10/2015		100.8
LB	F	FL	OI	29/05/2012		59.3
DL	M	FL	YI	08/08/2014		73.8
VK	M	VE	OI	15/01/2013		106.3
DG	M	KL	OI	17/12/2012		87.7
AS	M	JA	YI	27/02/2014		90.5
PU	F	HI	OI	20/03/2012		86.2
FR	F	HI	YI	03/09/2015		84.7
SH	M	PC	OI	08/03/2012		82.9
XT	F	PC	YI	28/09/2015		59.1
PN	F	TG	YI	28/04/2015		76.7
TZ	F	ML	OI		2013	82.1
AP	M	AE	YI	27/04/2014		71.6

F female, *M* male, ? unknown mother, *MA* mature, *OI* old immature, *YI* young immature

[a] Birthday for individuals born within the group; the year of immigration to the group is shown for those individuals that were not born within the group

interaction and contact calls are loud enough to be detected easily. The identities and time of all individuals joining (fusion) and leaving (fission) the sampled subgroup were monitored continuously, ensuring the calculation of the time that each individual spend in the same subgroup with each other. To secure the reliability of the identification of all sampled individuals, the observer (MBJ, systematically positioned in the center of the area occupied by the subgroup) was assisted by one to three experienced research assistants who were distributed all around in order to have visual access to all subgroup members. Assistants helped with the tracking and the identification of the individuals.

All grooming events were scored to obtain measures of social affinity. A grooming event consists in one or several directional grooming acts separated by pauses of a maximum duration of 10 s (Manson et al. 2004). We recorded all contact calls produced by the individuals using a directional microphone (Sennheiser ME 66) and a digital audio recorder

(TASCAM DR70D) on WAV files (sample rate 44.1 kHz, resolution 16 bit). In most cases, callers were located at 10 to 30 m from the microphone. We failed to identify callers of our observed subgroup in 157 occasions. All recordings were done and analyzed by the same observer. We collected a total of 512 h of acoustic recordings (36 h of observation were done without acoustic recording, due to unfavorable weather conditions, but we could still note the call utterances). We thus recorded a total of 1491 high-whinnies and 1848 whinnies from mature individuals (mean ± standard deviation; high-whinnies 74.5 ± 55.9; whinnies 92.4 ± 64.8 per individual), and a total of 674 high-whinnies and 68 whinnies from immature individuals (mean ± standard deviation; high-whinnies 42.1 ± 36.2; whinnies 4.2 ± 3.9).

Call classification

The two contact call types were identified by examining their acoustic structure and sound (Fig. 1). Both high-whinny and whinny calls are composed by a series of repeated, frequency modulated elements; however, high-whinnies have a higher fundamental frequency and broader bandwidth, while whinnies are characterized by intermingled grunt-like acoustic components that appear as abrupt drops and climbs of the fundamental frequency (Eisenberg 1976; Ramos-Fernández 2005, 2008).

A pre-classification was done in the field when recording the vocalizations, and the categorization was later confirmed directly on the computer screen using spectrograms in Raven PRO 1.5 (Bioacoustics Research Program, Cornell Laboratory of Ornithology). Spectrograms were drawn with a Fast Fourier Transformation (FFT, Sampling frequency 44.1 Hz), using a Hann window and an overlap time grid set at 49.9%.

To confirm the correct classification between whinnies and high-whinnies (based on Ramos-Fernández 2008), we conducted two analyses. First, we performed a classification reliability test (following Ouattara et al. 2009b). We randomly selected a subset of the original database (100 whinnies calls and 100 high-whinnies calls). Then, the observer (MBJ) classified the 200 calls into whinnies or high-whinnies. All sound files were anonymized before reclassification, and presentation of the 200 calls followed a random order. The procedure was repeated three times on separate days. We thus confirmed a high intra-rater agreement with Cohen's kappa tests (Cohen's kappa 0.70, 0.74, and 0.72, on three separate days; over 0.61 is considered as a strong agreement, Landis and Koch 1977). This demonstrates that the two call types can

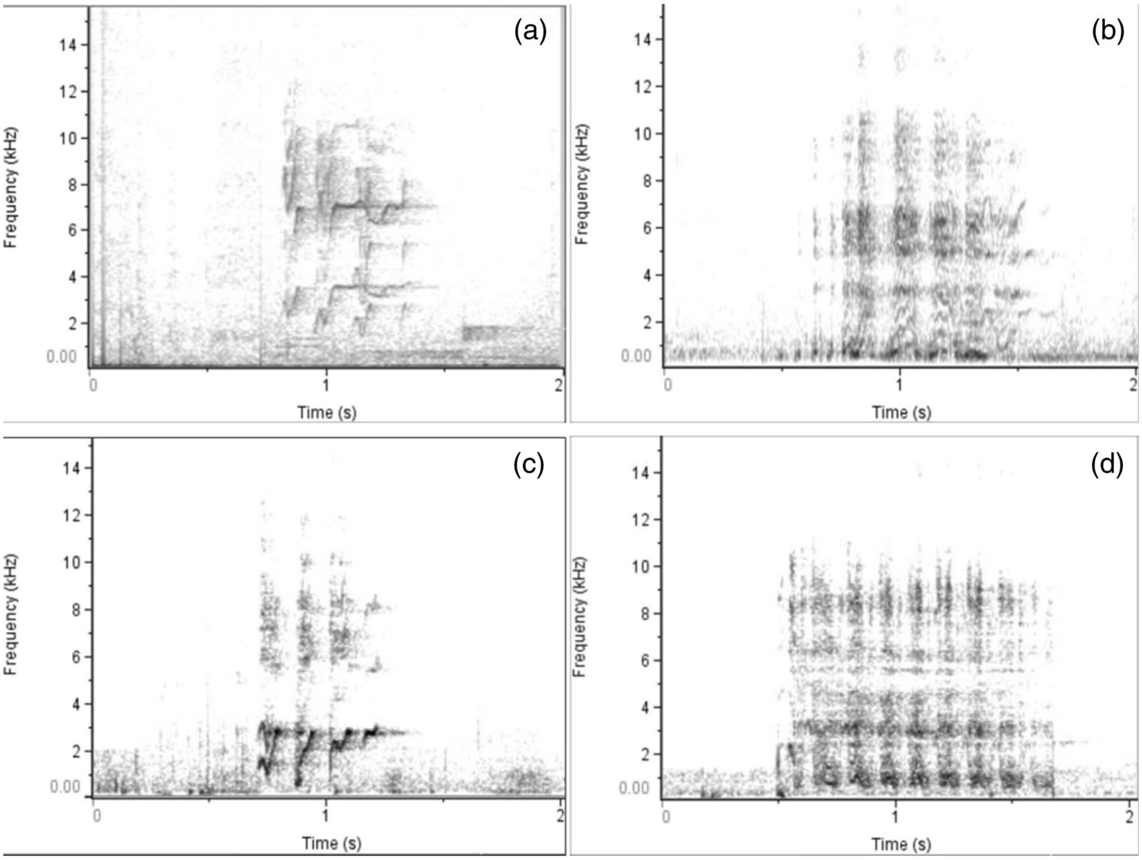


Fig. 1 Spectrograms of High-whinny (a), (c) and Whinny calls (b), (d) from a mature female (a), (b) and a mature male (c), (d) spider monkey (*Ateles geoffroyi*)

be categorized with little error by an observer using spectrograms.

A second analysis was performed to test for differences in the fine structural characteristics between call types (using IBM SPSS software). We randomly selected a sample of 100 whinnies and 100 high-whinnies emitted by ten individuals, three immatures (two males, one female), and seven matures (two males, five females). We selected nine representative acoustic parameters (see variables and definitions in Table 2, following the work of Chapman and Weary 1990; Ordóñez-Gómez et al. 2018). We confirmed, by visually inspecting box plots, that the variances of our parameters were sufficiently homogeneous. We transformed these nine variables into a set of non-correlated components using principal component analyses (PCA). To determine the number of relevant components (PC) for each call type, we used the Kaiser-Guttman criterion (keep only PCs with eigenvalues > 1). We thus identified two relevant components that explained 69% of the total variability (Table 3). We ran a MANOVA analysis using these components. This confirmed that call types can be significantly discriminated by their acoustic characteristics ($F_{12,187} = 4.8$, $P < 0.001$). Finally, in order to assess further the contribution of each acoustic parameter in the discrimination between call types, we performed a discriminant function analyses (DFA) (Fig. 2). The percentage of correct classification was higher than expected by chance (70%), and whinny and high-whinny had 74% and 67% chances respectively to be randomly well classified. The acoustic parameters that contributed the most to the classification were the Highest frequency (High Freq, Hz: LD1 = 8.96) and third quartile frequency (Q3freq, Hz: LD1 = 7.84).

Vocal behaviour analysis

As we were interested in vocal exchanges, we had to determine when a given call could be considered as a “response” to another call. Figure 3 shows the frequency distribution of inter-call durations (i.e., measured between pairs of consecutive calls emitted by different individuals). We considered that a call was emitted in response to another when the second one occurred within 3 s of the first (based on the method proposed by Lemasson et al. 2010, 2018). When more than one individual responded, only the first call in response was included in the analysis, as it was not possible to know who the third caller was responding to (as in Lemasson et al. 2018). We recorded the number of calls, identity of the caller (individual that produced the first call), and identity of the second caller (individual that responded). We recorded all vocal exchanges, but if the vocal exchange was between distant individuals (i.e., different subgroups), a non-identified caller was scored. We sampled a total of 1126 vocal responses (mean ± standard deviation; high-whinnies 13.9 ± 9.5; whinnies 17.4 ± 18.9).

We then calculated the following variables: *Individual call rate*, number of calls emitted by individual per observation time (h). We calculated this variable for each call type. *Individual response rate,* number of vocal responses emitted per observation time (h). We calculated this variable regardless of the call type and identity of respondent. *Dyadic response score (directional)*, number of times individual A responded to individual B divided by the time individuals A and B spent together in the same subgroup. *Dyadic affinity score* (*directional*), number of times individual A groomed individual B divided by the time individuals A and B spent

Table 2 Acoustic measurement definition. We used standard variables included in Raven Pro 1.5

Acoustic parameter (abbreviation, unit)	Definition
Maximum frequency	Maximum frequency of fundamental frequency (lowest frequency of a periodic waveform, F0) (Hz)
Minimum frequency	Minimum frequency of fundamental frequency (lowest frequency of a periodic waveform, F0) (Hz)
End of F0 (Hz)	The end of the frequency of the last fundamental frequency modulation (Hz) (based on Ordóñez-Gómez et al. 2018)
Lower frequency	The lower frequency bound of the call (Hz)
Highest frequency	Highest frequency (Hz). The upper frequency bound of the call
Third quartile frequency	The frequency that divides the call into two frequency intervals containing respectively 75% and 25% of the energy distribution (Hz)
Bandwidth	The difference in frequency between the frequencies intervals than contain 5% and 95% of the energy in the call (Hz). This variable corresponds to the variable bandwidth 90% in Raven Pro 1.5.
Peak frequency	The frequency with the highest energy in the call (Hz). This variable corresponds to the variable Max frequency in Raven Pro 1.5.
Duration	The total duration of the call in seconds measure as the temporal difference between the beginning and the end of the call. This variable corresponds to the variable Delta time Raven Pro 1.5.

Table 3 Principal component analysis performed on nine acoustic variables of Spider Monkey's contact calls (whinny and high-whinny). Eigenvalues and the percentage of variation explained for each component are shown for each component. Variables with the strongest loading are shown in bold font

Variable	PC1	PC2
LowFreq	*0.95*	− 0.12
HighFreq	− 0.17	*0.78*
BW90	− 0.15	*0.83*
Q3Freq	*0.70*	0.57
MaxFreq	0.19	*0.50*
DeltaTime	− 0.05	*0.33*
MinF0	*0.95*	− 0.05
MaxF0	*0.96*	− 0.01
EndfreqF0	*0.97*	− 0.05
Eigenvalue	*4.20*	2.00
Variance (%)	47.26	22.21

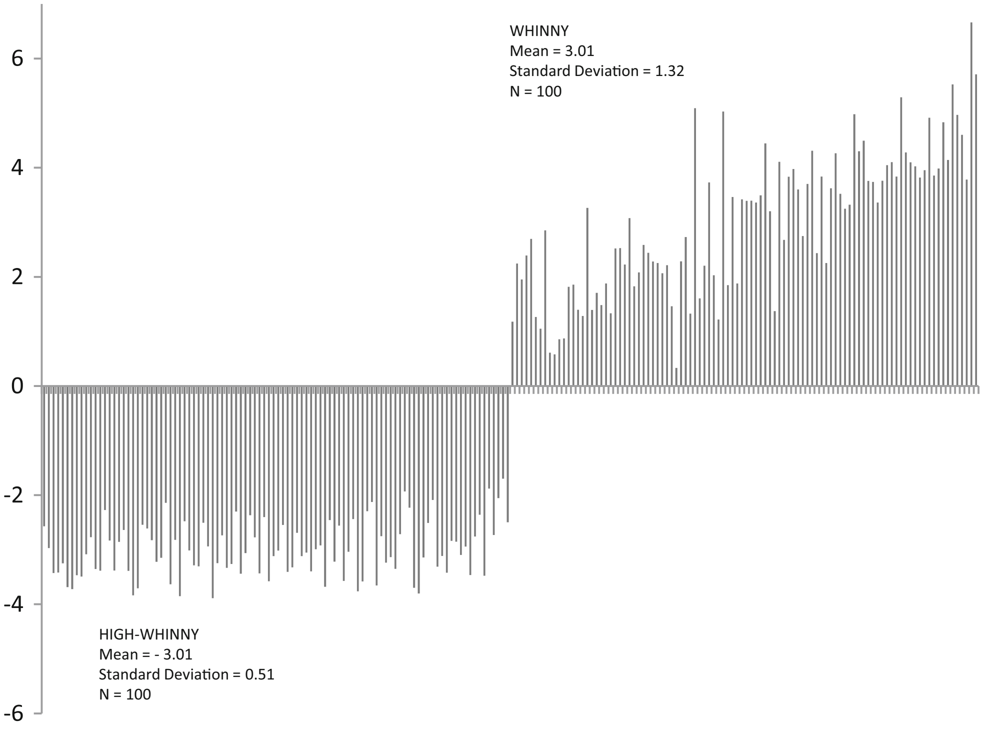
together in the same subgroup (as in Arlet et al. 2015). *Call matching*, number of instances that the first call was matched by the receiver. *Call non-matching*, number of instances that the first call was not matched by the receiver.

Statistical analysis

We built multiple linear regression models (MLR) and generalized linear mixed models (GLMMs), using the *lme4* package (Bates et al. 2014) in R (R Core Team 2016), to address all our research questions. For MLR, we checked homogeneity of variances and normal distribution of residuals, using fitted vs. residual plots and quantile–quantile plots for the residuals (Bolker et al. 2009). For all the GLMM models we built, a null model including the random factors only and a model including additionally the fixed effects. We compared the null and full model using a likelihood ratio test (LRT) with the ANOVA function (Zuur et al. 2009). We selected the full model as the final if the LRT was significant. We performed Tukey post hoc comparisons with the *multcomp* package (function *glht* in R, Hothorn et al. 2008) to detail the effects of factors and the *lsmeans* package (lsmeans function in R, Length 2013) to investigate the effect of interaction terms.

Firstly, we assessed the *influence of callers' characteristics on contact call rates*. A MLR was used to predict if age and sex classes of callers influenced individual call rates (i.e., number of calls per individual per hour of observation). Individual call rates were square-root transformed and normality of residuals was checked afterwards. We also tested the influence of callers' characteristics, principally age, on individual call rates and on the relative proportion of both call types (whinny VS high-whinny). We used a binomial logit link function (Bolker et al. 2009) to assess whether the caller's age and sex also influenced the relative proportion of both call types emitted per individual (GLMM1). Individual identities, date and time of the day (morning/afternoon) in which the call was recorded were included as random factors. Secondly, we evaluated the *influence of callers' characteristics* on their propensity to respond to others' calls. A multiple linear regression was used to predict if age- and sex classes of callers influenced

Fig. 2 Canonical score plot from function discriminant analysis of High-whinny and Whinny calls



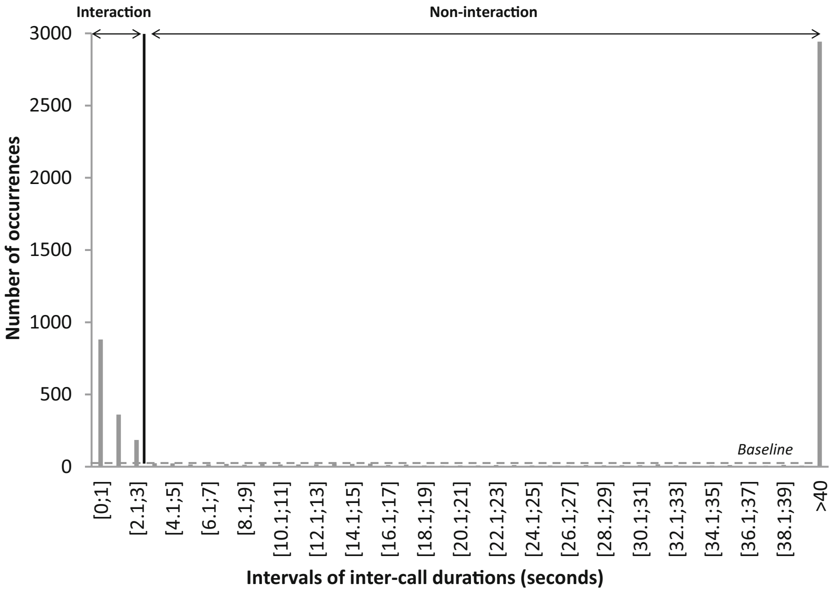


Fig. 3 Frequency distribution of inter-call intervals of spider monkeys (*Ateles geoffroyi*). The dotted horizontal line corresponds to the baseline of the occurrence of inter-call durations. The plain vertical line, delimiting interactions from non-interactions, was placed at the time where inter-call delays start rising above the baseline. The consecutive calls emitted by two different individuals typically trailed each other with less than 3 s

individual call response rates (i.e., number of responses per individual per hour of observation). Individual call rates were square-root transformed and normality of residuals was checked afterwards. Additionally, for immature individuals only, we tested the association between individual response rates and absolute age (in months) using a Spearman test.

Thirdly, we assessed the influence of the callers' characteristics on the vocal response patterns and whether individuals respond preferentially to certain partners. Since our target-dependent variable was the dyadic response score, we ran GLMMs using a Poisson distribution with a log-link function (Bolker et al. 2009) (GLMM2). The fixed effects were the second caller (respondent)'s age and sex classes in interaction with the dyadic affinity score. We included as random effects the first caller (initiator) identities, sex and age classes. Post hoc comparisons were done by *lsmeans* function where a significant result is indicated in the interval (asymp.LCL / asymp.UCL) not including zero. Additionally, we ran Spearman tests to evaluate the relation between dyadic affinity scores and dyadic call responses for each age-class without including mother-offspring dyads (since we were interested in social - non-maternal - affinity).

Fourthly, we assessed the *influence of caller's age on call type matching behavior.* We used a GLMM to test the influence of the caller's age on its propensity to respect call type matching when responding to a group member (GLMM3). Since our dependent variable was the presence (1) or absence (0) of matching in the vocal responses, we used a binomial logit link function (Bolker et al. 2009). The fixed effect was the second (respondent) caller's age sex class. We included as random factors the sex of the second caller, the identity, the age-class and the sex class of the first (initiator), caller and the time in which the vocal exchange was recorded (morning/afternoon).

For Poisson and Binomial models, we checked the assumptions of the full models calculating Variance Inflation Factors - VIF (Kulik et al. 2016) for each model. The VIF' values indicated the absence of collinearity (values should be ideally bellow 4). Largest VIF were respectively: 1.01 (GLMM1), 1.5 (GLMM2) and 1.1 (GLMM3). Additionally, we tested for overdispersion using the *blmeco* package (function *dispersion.glmer* in R, Korner-Nievergelt et al. 2015). The dispersion' values indicated the absence of overdispersion (values should be ideally around 1): 1.2 (GLMM1), 0.82 (GLMM2) and 0.97 (GLMM3). We also tested stability for each model by comparing the estimates derived from a model based on all data with those obtained from models without identified influential individuals (based on Cook's distance, influence.ME package, Nieuwenhuis et al. 2012). All the models are still significant after this procedure.

Data availability

The datasets used in this study are available from the corresponding author on reasonable request.

Results

Influence of caller's age on contact call rates

Caller's age significantly influenced its overall call rates (LMM: F (2, 1) = 30.6, $P < 0.0001$; Fig. 4). Sex had an almost significant effect as well (LMM: F (2, 1) = 3.6, $P = 0.06$). Post hoc Tukey comparisons showed that adults called more often

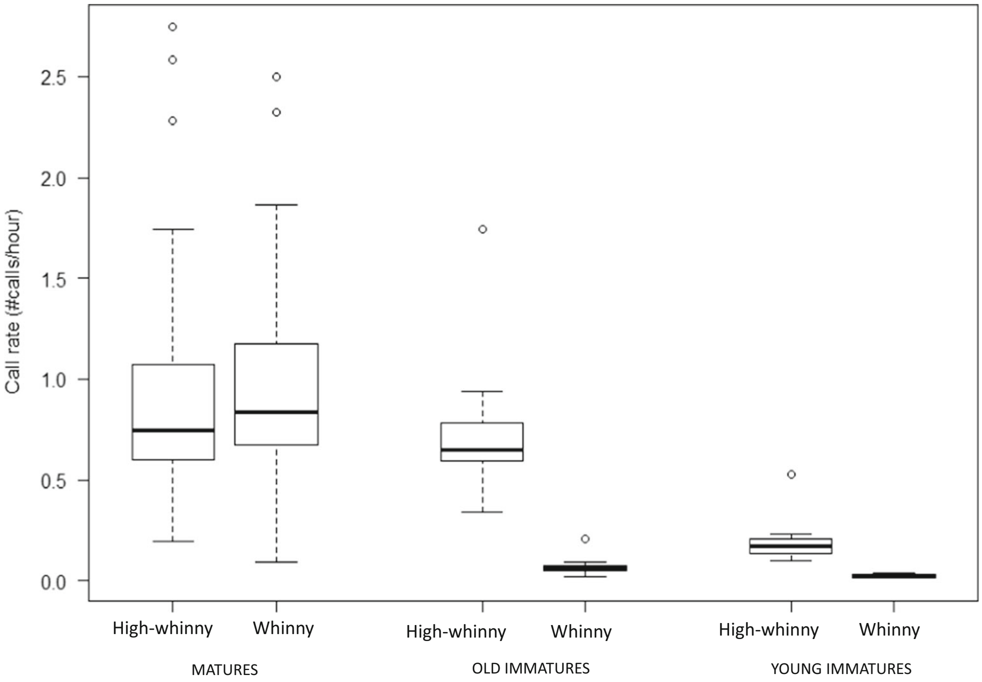


Fig. 4 Call rates of mature (N = 20) and (old and young, respectively $N = 8$ and $N = 8$) immature spider monkeys (*Ateles geoffroyi*). The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and outliers

than both young ($\beta = -0.9$, SE = 0.1, $Z = -7.2$, $P < 0.001$) and old immature ($\beta = -0.5$, SE = 0.1, $Z = -3.8$, $P = 0.001$) individuals, and that old immatures called more often than young immatures ($\beta = 0.4$, SE = 0.1, $Z = 2.8$, $P = 0.02$).

The relative proportion of both call types also changes along development, since our full model was significantly different from the null model (LRT: $\chi^2 = 48.6$, $P < 0.0001$; Fig. 4). Caller's sex was not significant ($\chi^2 = 1.2$, $P = 0.3$), contrary to caller's age ($\chi^2 = 90.4$, P < 0.0001). Post hoc Tukey comparisons showed that young ($\beta = 2.3$, SE = 0.5, $Z = 4.9$, $P < 0.0001$) and old ($\beta = 3.0$, SE = 0.3, $Z = 8.8$, $P < 0.0001$) immatures presented higher proportions of high-whinny (compared to whinny calls) than matures. However, young and old immatures did not differ in this regard ($\beta = 0.7$, SE = 0.5, Z = 1.4, $P = 0.3$).

Influence of caller's age on vocal response rates

Our linear model showed that caller's age (LMM: F (2, 1) = 61.2, $P < 0.0001$) and sex (LMM: F (2, 1) = 7.4, $P = 0.01$) significantly influenced its overall vocal response rates. First, females responded more often than males. Second, post hoc Tukey comparisons showed that adults responded more often than both young ($\beta = -0.2$, SE = 0.05, Z = − 5.1, $P < 0.0001$) and old immature ($\beta = -0.5$, SE = 0.05, Z = − 10.2, $P = 0.0001$) individuals, and that old immatures responded more often than young immatures ($\beta = -0.2$, SE = 0.06, Z = − 4.4, $P = 0.0003$) (Fig. 5). When focusing on immature individuals' absolute ages, we found a positive correlation with older individuals showing higher response rates (Spearman test: $r = 0.8$, $P < 0.0001$) (Fig. 6).

Influence of caller's age and social affinity on vocal response patterns

The choice of specific vocal partners emerged when maturing. Our full model was significantly different from the null model (LRT: $\chi^2 = 349.6$, $P < 0.0001$). The callers' age in interaction with the dyadic affinity scores significantly influenced the dyadic responses scores ($\chi^2 = 75.13$, $P < 0.0001$), again sex was not significant here (LRT: $\chi^2 = 0.99$, $P = 0.3$). Post hoc Tukey comparisons showed that adults responded more often to individuals they often groom than did old ($\beta = 12.2$, SE = 0.7, $Z = -4.4$, intervals 95% CI = 10.8–13.5) and young ($\beta = -144.0$, SE = 85.3, $Z = -4.4$, intervals 95% CI = − 311.3–− 23.2) immatures. No difference was found when comparing young and old immatures ($\beta = 1.8$, SE = 1.0, $Z = -4.4$, intervals 95% CI = − 0.1–3.8).

Influence of caller's age on call type matching behaviour

Call type matching became more systematic along development (Fig. 7). Our full model was significantly different from the null model (LRT: $\chi^2 = 19.1$, $P = 0.0003$). The model showed that caller's age significantly influenced call type matching behaviour ($\chi^2 = 22.6$, $P < 0.0001$), but sex did not ($\chi^2 = 1.9$, $P = 0.16$). Post hoc Tukey comparisons showed that adults responded more often with the same call type than did young ($\beta = -1.2$, SE = 0.36, Z = − 3.2, $P = 0.003$) and old ($\beta = -0.8$, SE = 0.21, Z = − 4.03, $P = 0.0001$) immatures.

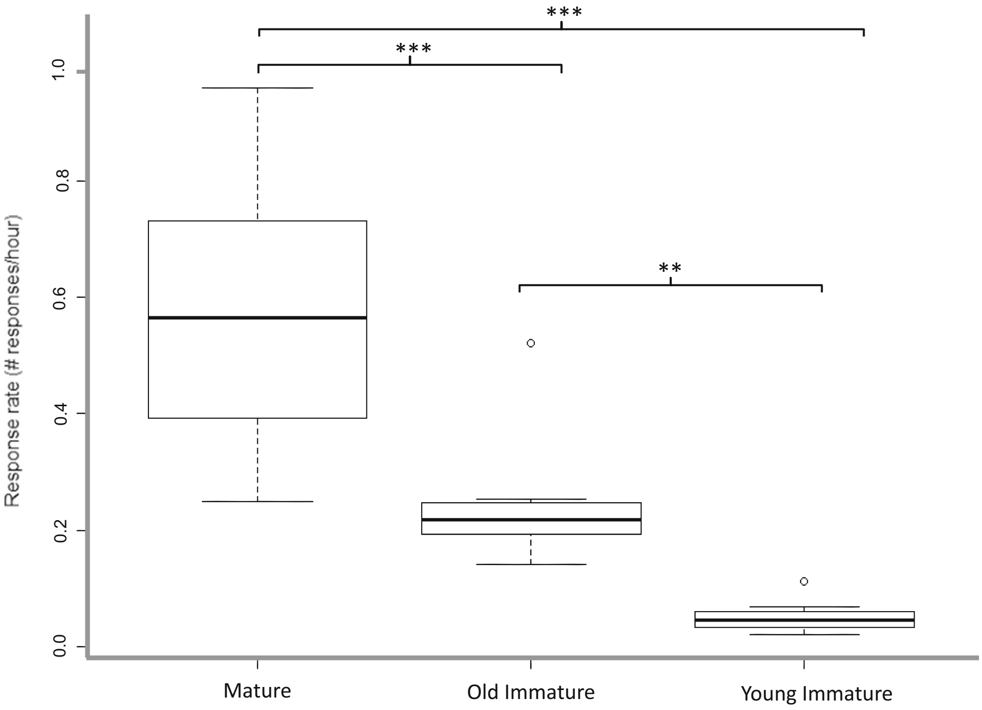


Fig. 5 Vocal response rates of mature ($N = 20$) and (old and young, respectively $N = 8$ and $N = 8$) immature spider monkeys (*Ateles geoffroyi*). The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and outliers. Tukey post hoc comparisons. $^{**}P < 0.001$; $^{***}P < 0.0001$

Again, we found no difference between old immatures and young immatures ($\beta = 0.33$, SE = 0.38, $Z = 0.87$, $P = 0.65$).

Discussion

We found an effect of age and social affinity in the use of contact calls by spider monkeys. Mature individuals showed higher call rates, higher vocal response rates, and higher proportions of call matching than immature individuals. Our results also suggest that vocal interaction in mature individuals occurred at higher frequency between individuals with higher social affinity. This pattern was also observed, to a lower extent, in immature individuals, and even less so for young than old immatures. Immatures did not pay attention to the call type and caller identity they were responding to, their contribution to vocal exchanges increasing with age. Together, these results show that variation in the use of different contact calls in spider monkeys relates to maturity and grooming affinity, suggesting that social learning could have

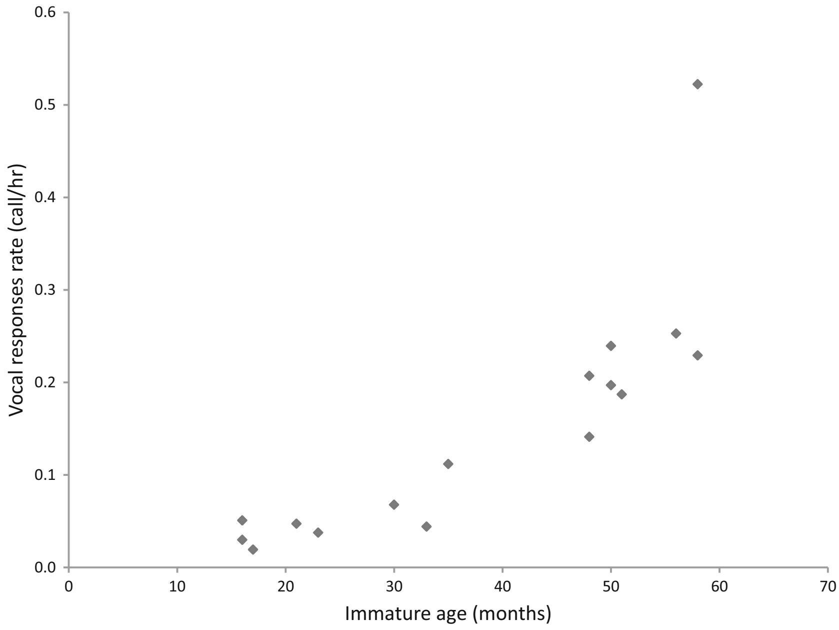


Fig. 6 Association between vocal response rates and age of immature caller spider monkeys (*Ateles geoffroyi*)

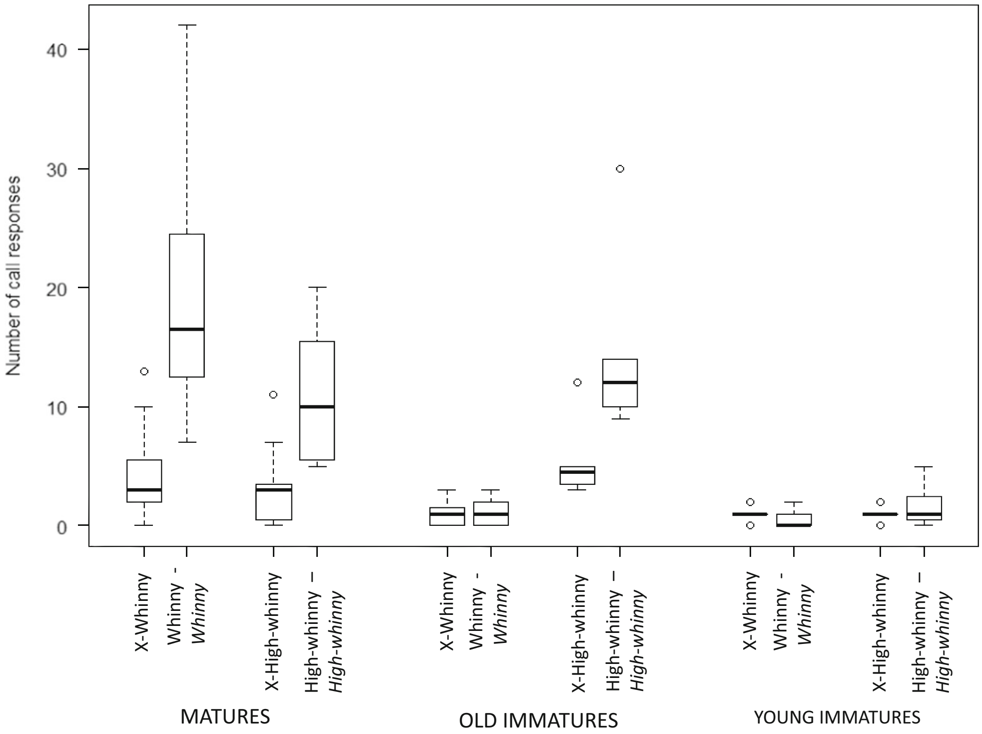


Fig. 7 Call matching and non-matching in mature (a), old (b), and young (c) immature spider monkeys (*Ateles geoffroyi*). *X-Whinny call*: the individual responds with a whinny call to a non-Whinny call. *Whinny call–Whinny call*: the individual responds with a Whinny call to a Whinny call. *X-High-whinny call*: the individual responds with a high-whinny call to a non-high-whinny call. *High-whinny call–High-whinny call*: the individual responds with a high-whinny call to a high-whinny call. The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and outliers

an important effect on vocal behaviors, producing "conversational rules" in adulthood.

Our findings support the existence of "conversational rules" respected by adult spider monkeys, as it has been found in several nonhuman primate species (Snowdon and Cleveland 1984; Symmes and Biben 1988; Lemasson et al. 2011a). One conversational rule typically found in other species is the contribution rate to vocal exchanges, which is age-dependent (Lemasson et al. 2010). Here, we found that adults vocalized significantly more and responded more often to each other than immature individuals. Call exchanges play an important role in maintaining a socio-spatial coordination of group members, and this is even more important in species with high fission-fusion dynamics that live in visually closed habitats as spider monkeys (Ramos-Fernández 2005). It was indeed found earlier that playbacks of whinny calls influence the behaviour of recipients depending on their social relationship to the caller (Ramos-Fernández 2005). As in other primate species (Lazaro-Perea 2001), mature should form the stable social core of the group and are thus in charge of the coordination, which could explains their high vocal activity (see also *Saguinus mystax*, Garber et al. 1993; *Callithrix jacchus*, Bezerra et al. 2009). Spider monkeys seem to follow a developmental pathway as that found in Japanese macaques, with call exchange rates increasing regularly with age (Lemasson et al. 2013b) and particularly when maturing (Koda et al. 2008). The pattern is also similar to that found in marmosets, in which a gradual emergence of vocal responses was found when comparing infants with juveniles and as well as when comparing juveniles with adults (Pistorio et al. 2006). Another explanation for the fact that immatures call less than mature individuals can be the quasi-constant proximity with their most preferred associate (mother). Caller's sex also influenced vocal response rates in our study, which is in line with previous work that showed that females are more vocally active than males in this species (Fedigan and Baxter 1984).

A second conversational rule found in other species is that the vocal interactions between individuals are not random but occurs preferentially with particular individuals. Our results show that as spider monkeys mature, their vocal interactions occur preferentially with their affiliative partners. This is similar to what was found in Japanese macaques (Arlet et al. 2015), bonobos (Levréro et al. 2015), and gorillas (Lemasson et al. 2018). In squirrel and Campbell's monkeys, as well as in common marmosets, experienced elders get more vocal responses than younger adults (Biben et al. 1986; Chen et al. 2009; Lemasson et al. 2010). In spider monkeys, it was experimentally shown earlier that whinnies elicit more responses from close associates of the caller than from other individuals (Ramos-Fernández 2005). These findings support the social bonding hypothesis suggesting that vocal exchanges would have evolved in primates to play the role of "grooming-at-a-distance" in order to facilitate the maintenance of social cohesion between individuals living in large and complex social groups (Dunbar 2003). Spehar and Di Fiore (2013) also suggested that vocal exchanges may help to maintain distance and avoid competition for food resources between individuals.

A third conversational rule found in other species is the use of an acoustically similar call to answer to a call, a phenomenon named call matching. This behaviour is found in several primate species (e.g., Chimpanzees, Mitani and Brandt 1994; Japanese macaques, Sugiura and Masataka 1995; Diana monkeys, Candiotti et al. 2012; Agile gibbons, Koda et al. 2013; bonobos, Levréro et al. 2015). Acoustic convergence is also typically observed during human conversations as described in the vocal accommodation theory (Giles et al. 1991). In some studies in non-human primates, authors compared juveniles and adults, and found, as here, that immature individuals do not systematically respect the conversational rules. For example, in Campbell's monkeys, immature individuals spontaneously broke the turn-taking rule 12 times more often than adults by calling twice in a row without waiting for another group member to respond (Lemasson et al. 2011b). Moreover, the authors showed that juvenile Campbell's monkeys do not behave differently when hearing playbacks of vocal exchanges respecting or not the turn-taking rules, whereas adults did (Lemasson et al. 2011b). Also, immatures sometimes show a lack of precision in the timing of their vocal utterance. Along their development, agile gibbons improve the precision of the song synchrony when duetting with their mother (Koda et al. 2013). Another example is given by the study of juvenile common marmosets (Chow et al. 2015) and chimpanzees (Laporte and Zuberbühler 2011) who progressively acquire the appropriate timing of response as well as the social target for their vocal responses. Japanese macaque subadults respected less than adults the call-matching rule during inter-individual exchanges of coo calls (Sugiura and Masataka 1995; Masataka 2003). In the same species, a playback experimental study demonstrated that juveniles failed to discriminate between a pair of matching (i.e., two calls given by two individuals with matched frequency modulation amplitudes) and a pair of non-matching coo calls, while adults did (Bouchet et al. 2017). Also, in Agile gibbons, older daughters match better the great call acoustic signature of their mothers than younger ones (Koda et al. 2013). Our results are in line with these findings, showing that younger spider monkeys do not follow adult rules. Mature spider monkeys matched their calls in a higher proportion than old immatures, who in turned matched more than young immatures. Call matching has been proposed to function in maintaining and strengthening social bonds, notably in species where group members are traveling in visually closed habitats such as chimpanzees (Mitani and Gros-Louis 1998) and guenons (Candiotti et al. 2012).

Overall, our results show that immatures and matures differ in terms of contact call rates and contextual usage of these calls. We suggest three non-mutually exclusive developmental hypotheses. Firstly, maturation (morphoanatomical) could explain the higher overall proportion of high-whinny contact calls in the youngsters' spider monkeys as a result of high whinnies being easier to produce for immature vocal tracts than whinnies. Whinnies consist of a series of rapid rises and falls in pitch (i.e., "arches"). Between the arches, other sounds called "interarch elements" are found, and their rapid alternation gives whinnies a "grunt-like" quality absent in high-whinnies (i.e., calls with no interarch elements). While it would seems as two kinds of sounds produced by different articulatory mechanisms, the interarch elements are due to a period doubling in laryngeal oscillation (see Ramos-Fernández 2008). This period doubling could be difficult to produce by immature vocal tracts, thus decreasing the frequency of whinnies in that developmental stage. Moreover, frequency parameters mostly depend on larynx size and are usually correlated with individual characteristics such as age and body size (Riede et al. 2005; Ey et al. 2007). In most species, juveniles do produce significantly higher-pitched units than adults (e.g., *Cebuella pygmaea,* Elowson et al. 1992; *Cercopithecus aethiops* and *Macaca mulatta,* Rukstalis and French 2005; *Cercopithecus neglectus*, Bouchet et al. 2012). This hypothesis, however, does not fully explain our findings because young spider monkeys produce whinnies, suggesting that the lack of maturation of the vocal apparatus does not restrict the production of low pitch calls in the species. Alternatively, the maturation of the auditory system and brain processing could also explain the poor control of the timing of the vocal utterances and the perception of the acoustic subtlety during exchanges (Takahashi et al. 2013). Secondly, motivation may explain some of our findings. Social interactions may not be as important in early stages of life as they are in adults, since immatures remain strongly influenced by their mothers' decisions (de Waal 1996). In line with this idea, we observed an increasing contribution to vocal exchanges with the age of immatures. We can indeed predict that arousal level increases when individuals that provide social support are farther. Thirdly, social learning may play another important role. Young monkeys may have to learn the appropriate usage of these calls. Immatures are indeed able to produce both call types in our study species, but only adults filter their emissions to vocalize with the appropriate acoustic structure in the appropriate context. Social learning has been clearly demonstrated in other New World monkey species, showing notably the crucial role of social feedback from adults during vocal development (Elowson and Snowdon 1994; Snowdon et al. 1997; Snowdon and Elowson 1999).

In a recent study, Ordóñez-Gómez et al. (2018) found that spider monkeys use up to five different contact call types depending on the distance between group members, a strategy that spider monkeys use to cope with the environmental propagation constraints of acoustic signals. Thus, some of these contact calls types are used to communicate at long distances (Ordóñez-Gómez et al. 2018). However, our conclusions on the conversational rules proposed in this study are based on contact calls that spider monkeys use in short-distances (i.e., communication between partners traveling in the same subgroup that could both be identified, exchanging partners being typically between 0 m and 60 m) and further studies are needed to understand whether this conversational rules apply to long-distance calls.

Our findings add to the literature suggesting that social learning of call production, usage, perception, and comprehension should be considered separately when studying vocal development in nonhuman primates as they certainly develop at different speeds and degrees. For example, both immature and mature individuals are able to produce the two studied contact call types but they do so differently. Adults respect rules, exchanging with specific partners and adjusting the acoustic structure of their response to the call they are responding to. This requires flexible abilities at usage (call timing), perception (call structure), and comprehension (caller identification) levels, abilities that emerge progressively during development before adulthood. Even if juveniles are often able to produce adult-like calls, they may need time and social experience before they can appropriately use these vocalizations (Seyfarth and Cheney 1986). Intergenerational vocal exchanges give the opportunity for immatures to practice and learn how to adjust calling to the species-typical pattern (Pistorio et al. 2006). While studies of social learning in the acquisition of the appropriate context of calling and appropriate response to others' calls have typically focused in specific call types known to have some sorts of referential function and emitted in narrow contexts (vervets and predator-associated calls, Seyfarth and Cheney 1986; cotton-top tamarins and food-associated calls, Elowson and Snowdon 1994; pigtail macaques and aggression-associated calls, Gouzoules and Gouzoules 1989; Japanese macaque and greeting-associated calls, Katsu et al. 2014), we suggest that changes in call usage styles (partly due to social learning) also concern calls emitted in a broad range of contexts. We believe that vocal development in nonhuman primates may be more widespread that often expected in nonhuman primates, and it deserves to attract more attention in the future. Studies need to try to better disentangle the combined effects of maturation and behavioral experience. All in all, this provides new insights into how vocal communication and social bonding co-evolved in the primate lineage (Bouchet et al. 2017).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Our study adhered to the legal requirements for field observations of animals in Mexico. Protocols were approved by the Direccion General de Vida Silvestre (SEMARNAT, permit #SGPA/DGVS/1405/15). The Direccion General de Vida Silvestre is a subdivision of the Mexican government that oversees the ethical treatment of wildlife and only authorizes studies where data is collected according to this treatment.

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