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Notes on a tree: reframing the relevance of primate choruses, duets, and solo songs

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The complexity of primates' singing behavior has long gathered the attention of researchers interested in understanding the selective pressures underpinning the evolution of language. Among these pressures, a link between territoriality, pair-living, and singing displays has been suggested. Historically, singing primates have been found in a few taxa that are not closely related to each other, and, in the last years, their phylogeny has dramatically changed. Hence, we aimed at understanding if the dogmatic association between territorial behavior and a monogamous social structure still holds in the light of current research. Moreover, singing behavior has often been considered a whole, but animals can perform different singing forms depending on how many individuals call simultaneously. Currently, it is unclear to which extent these singing forms are widespread among these primate groups. Given that there is no unique definition for a *song*, *solo*, *duet*, and *chorus*, we envisioned some of the most used descriptions. We then formulated some new definitions that we followed in our review of the presence/absence of these different forms of song organization among singing primates' taxa. In particular, we suggested that tarsier species that are typically considered non-singers may indeed sing, and we pointed out that non-duetting gibbons may perform duet interactions. We found that, besides duets, chorusing behavior and solo songs are essential features of primates' communication, but their study is still in a descriptive phase. Moreover, while territorial behavior seems to be conserved in these singing taxa, we highlighted that the monogamous social structure is not the rule. Pair-living plus multi-females groups displaying singing behavior are common too. We suggest that ending to consider these taxa as uniform in their sociality and vocal behavior might be a significant turning point to unravel the different selective pressures that influenced the emergence and organization of such peculiar vocal behavior.

KEYWORDS: singing, tarsiers, gibbons, titi monkeys, indris, territorial, pair-living, phylogeny.

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Reframing the relevance of primates' songs

Introduction

Among the diversity of primates' vocal signals, the most complex and intricate displays are those related to singing behavior (Ravignani et al. 2014). While many primate species make conspicuous use of vocalizations, a limited number of taxa communicates using combined or stereotyped sequences of long-range vocal emissions, usually termed songs. There is no unique definition of song, but most authors agree to distinguish it from a vocalization considering the duration, the typical frequency modulation, and the apparent temporal and structural hierarchy between song elements that are not combined randomly but form a precise sequence in time (e.g., Spector 1994). Mammals' song production is limited (Haimoff 1983), and about 16% of primate taxa have grouped within the singing primates (Gamba et al. 2014; Haimoff 1986). Historically, singing primates have been found in the Hylobatidae family, in the Indriidae family (only in the genus *Indri)*, in the Tarsiidae family, and in some genera of the Pitheciidae family (Robinson 1979; MacKinnon & MacKinnon 1980; Haimoff 1986; Niemitz et al. 1991; Geissman 1993; Thalmann et al. 1993). These primates are not closely related (Fig.1A, 1B); thus, it is likely that singing behavior has independently evolved within the order (Geissmann 2000).

The hypothesis of an independent evolution is intriguing since it is unclear which drivers led to this peculiar behavior in species that show such diverse traits. These primates can be nocturnal or diurnal, folivorous and faunivorous, and have very different morphologies. Their singing behavior has been associated with a territorial and socially monogamous lifestyle (Geissmann 2000). It has been hypothesized that the evolution of long-range coordinated signals has been guided by the stability of resources over the years, favoring resource acquisition via territorial defense by a stable collaborative group, as it has emerged from studies on birds (Thorpe 1963; Logue & Hall 2014; Tobias et al. 2016). Geissmann (2000) suggested that the evolution of primates' singing behavior could be related to the development of monogamy, which involves a pair-living social system. Currently, it is not clear to what extent territorial defense and pair-living social structure are shared among singing species. Hence, our first aim was to explore to what extent pair-living and territoriality are widespread among singing species of primates, according to recent studies. In fact, there is increasing evidence speaking against the pair-living social organization in singing primates as a rule (e.g., Barca et al. 2016).

Moreover, "singing behavior" has often been considered as a whole. Still, different forms of singing can take place, depending on how many individuals perform the vocal display simultaneously (Fig. SM1), and there is no clear picture of how much these forms are spread among singing primates' groups. Thus, our second aim was to map the occurrence of solo songs, duets, or choruses across the singing taxa in association with their social and mating system and territoriality. Hence, we provide the first review about primate singing displays and re-analyzing the traits indicated as potential factors that led to the evolution of singing. After revising the most used definition for song, solos, duets, and choruses, we propose a new definition for the terms *song* and *chorus*. We reported the detailed information we found (see Supplementary Material), either at the mating system level (e.g., monogamy, polygyny) or social system level (e.g., pair living, multi-females). However, many data are missing as singing primates are extremely challenging to study. They live in dense tropical forests, generally with low population density. Also, only a few individuals and species are available for ex-situ studies (gibbons, Melfi 2012) given the difficulty, or impossibility, to breed them in captivity (tarsiers, Řeháková-Petrů 2019; indris, Petter et al. 1977).

Towards new systematics of singing

Song. Most authors agreed on differentiating songs from calls—the first showing remarkable duration, complexity, and the presence of notes, also called units or elements (Spector 1994). In songs, emitter(s) utter units following a precise temporal pattern. This temporal regularity is a crucial feature highlighted in most definitions. Thorpe (1961) described the birdsong as “a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence of pattern in time”. Geissmann (2002) and Haimoff (1986) adopted Thorpe’s (1961) definition when rereferring to the gibbons’ song. This definition is particularly suitable, focusing on the utterance’s spectral and temporal features rather than its function and ontogeny (Logue & Krupp 2016; Catchpole & Slater 1995). It is unclear to what extent songs’ functions are shared between different singing species. Thorpe’s criteria would also easily separate songs from loud calls: roaring bouts of howler monkeys, for example, are composed of a series of harsh and chaotic emissions, where melodic features are absent (Ybarra 1986). We hence propose that songs can be defined as a series of notes of different types, uttered following a hierarchical structure (Fee and Long, 2013), and characterized by a frequency variation. Singing may occur with different degrees of interaction with conspecifics, and we can then recognize solos where only a singer is involved (Seddon 2002), duets which is a dyadic interaction (de Reus et al. 2021; Fig. SM1A, B), and choruses that include multiple singers (e.g., birds, Seddon 2002; primates, Raemaerkers et al. 1984; Fig. SM1C).

Solos. Solo songs have generally been considered as a series of two or more syllables given by a single individual (Seddon 2002, adapted from Farabaugh 1982). A critical point when studying solos is the understanding of solo singing vs a duet contribution unanswered by the partner. For example, by answering each other’s songs, paired birds prevent solo singing, advertising the mated status of their partner (Langmore 1998). Consequently, if a pair member does not answer, the result would be the other member emitting a solo song. This case is quite different from what happens, for example, in Bornean gibbons (*H. muelleri*). Males emit solos and duets at specific times of the day: solos before dawn, while duets with females occur later (Clink et al. 2020). For this reason, we point out that a solo derived from the absence of a reply from a pair member (*unanswered duet*) should be considered different from a solo song that is usually emitted by a single individual (*solo singing*). However, in the present work, we will not differentiate between these two categories due to the lack of information on the context in which these songs are emitted.

Duets and choruses. A vocal duet is an acoustic interaction between two partners (Bailey 2003), whether they emit simple calls or more complex vocal displays. In avian studies, pair-mates typically interact in duets, which were regarded as joint vocal displays in which breeding pairs sing in combination with one another, either synchronously or alternately (Thorpe 1972; Farabaugh 1982). In birds, male-male duets (Trainer et al. 2002) or juveniles performing with adults of the opposite sex were also observed (Seddon 2002). For this reason, as suggested by Langmore (2002), a more suitable definition of duet should consider spectro-temporal properties rather than the identity of the emitters, which define the type of interaction. Hall (2009), for example, proposed that a duet is emitted by two individuals that coordinate their singing so that their phrases would alternate or overlap. To differentiate this particular behavior from a general two-individual vocalization (e.g., the calling of crickets, Zimmermann et al. 1989), we will refer to the coordinate song emission between two individuals as a duet song. Primates emit duets either with their partner or with an offspring of the opposite sex (e.g., indris, Gamba et al. 2016), or with an adult and an offspring of the same sex, often mother and daughter (e.g., gibbons, Raemaerkers et al. 1984). In these vocal interactions, daughters try to synchronize their vocal utterances to match the mothers' ones, which has been supposed to be a practicing process (Koda et al. 2013). It is intriguing that this particular kind of duet also occurs in species of gibbons that do not show duetting behaviour (Kappeler 1984). Even if duets between members of the same sex in indris do not happen, juvenile females can sometimes match their mothers' notes in the duet emitted by the mated pair (De Gregorio, *pers. obs*.). While these cases would satisfy the criteria defined by Langmore (2002) and Hall (2009), we asked ourselves if would be the case of differentiating, at least for singing primates, same-sex duet as *song matching duets* and opposite-sex duets as duet songs. This distinction may have also sense in light of the dramatic differences in temporal structure between the two duet types: total synchronization in the matching, from antiphonal to partial overlap in different sex duets.

In singing primates, offspring of the reproductive pair may join the duetting adults creating a family chorus. In the last decades, the term chorus has been widely used to indicate various vocal displays, united by having more than two individuals emitting acoustic signals simultaneously (Gerhardt & Huber 2002). Different studies refer to the term chorus as the simultaneous emission of the same call type by more than two animals, either in a cacophonic or synchronized way (Yoshida & Okanoya 2005; Pika et al. 2018). In birds, the term chorus has been used either to refer to the simultaneous, cacophonic display of different birds emitting song in the same time of the day ("bird dawn chorus", Gil & Llusia 2020) and the communal singing that takes place when two or more birds coordinate their emissions (Seddon 2002; Hale 2006). This can happen when a juvenile joins the parents' duet (Seddon 2002), similar to what occurs in singing primates. While the "dawn chorus" and duetting behavior of birds have been extensively investigated, the chorusing of different individuals from the same group remains little studied. As for birds, the term chorus has been used to indicate both a display of a primates' group or the contemporary song emission by several primates' groups or individuals of different groups. Haimoff (1986) described as chorus also the calls of one animal or the duet being sequentially followed by others, like howler monkeys (despite it is considered that they produce rather loud calls than songs), siamangs and gibbons; moreover, some studies on gibbons defined as a chorus the emissions at the dawn of male solo songs from different groups (Tenaza 1976). Since duet songs imply complex turn-taking processes between the two emitters, we suggest that a chorus song cannot be only defined by the temporal proximity of more than two song events. For this reason, in this review, we referred to "chorus song" as the coordinated emission of songs displayed by more than two individuals within the same group members. In singing primates, in many cases, a chorus song is uttered by the mated pair and their offspring. In some cases, juveniles tend to match the adults' utterances while the parents are duetting (Merker and Cox 1999; De Gregorio *pers. obs.*)

The participation of the juveniles in the adult song display has no apparent function yet, but it may represent a form of practicing towards a fully adult-like song (Koda et al. 2013; De Gregorio et al. 2021) and an occasion to broadcast their individuality (Gamba et al. 2016).

Social systems and mating systems

While the social system of a species indicates who lives with whom, its mating system indicates who mates with whom. Among the social systems, pair living is the one that has been typically linked to a monogamous mating system, and it has been described as two adults of the opposite sex living together in their home range with their non-reproducing offspring (Tecot et al. 2016; Huck et al. 2020). Following Huck and colleagues (2020), a pair living social system can have a sexually monogamous mating system when an exclusive mating relationship between a single female and a single male take place, or a genetic monogamous mating system when a female and a male reproduce exclusively with one another over a set of multiple births. However, "monogamy" is an ambiguous concept that has been often used in referring to either a social or a mating system (Fernandez-Duque et al. 2020). In fact, when revising the literature, we found some inconsistencies in the usage of the word "monogamy", and only a few studies reported observations of copulations and genetic analysis to assess with certainty the presence of a particular mating system. Thus, if "monogamy" should be used when referring to an animal's mating behavior (Huck et al. 2020), when clear information about this trait lacks one should only report the species' social organization. Thus, in our cross-taxa comparison, we considered only this attribute (e.g., *noyau*/solitary, pair-living, multi-males/females) to avoid confusing the social and the mating levels. However, we reported in Supplementary Material all the detailed information we found on both social and mating systems, using the original terms used in the original works (e.g., "monogamy", "genetic monogamy", "social monogamy", ...).

Overview

Tarsiers. The family Tarsiidae includes small-bodied, nocturnal, and faunivorous primates (Schwartz 2003), classified in three genera (Groves & Shekelle 2010): *Tarsius* is found in Sulawesi (12 species), *Cephalopachus* in Sumatra and Borneo (one species), *Carlito* on islands of the southern Philippines (one species). However, more species will likely be identified (Shekelle et al. 2017). Singing behavior is well known in the gen. *Tarsius*, where male and female emit a duet song (Gursky et al. 2017; Fig. SM1F, Tab. SM1), even if spectrograms of pygmy tarsier's duets (*T. pumilus'* - Grow et al. 2016) seem to lack a precise hierarchical structure and different note types resembling more a multi-individual vocalization than a duet song. However, further acoustic analysis investigating the note modulation and organization would assess this duet structure. Besides, members of genera *Carlito* and *Cephalopachus* do not sing a duet (Groves & Shekelle 2010). Even so, since we did not find any mention of singing behavior, do they sing at all (Fig. 1B, 1C, Tab. SM1)? The acoustic repertoire of Philippine tarsier (*C. Syrichta*) comprises two vocal behaviors that may have the potential to be classified as solo songs: a) a series of different calls often occurring in a sequence, and b) trills, complex, harmonic calls consisting of several modulated notes (Řeháková-Petrů et al. 2012). For the present study, we considered this species as non-duetting but as *data deficient* for solo songs. We suggest that further analyses may conclude that singing behavior is likely to be present. The calls of the Horsefield's tarsier (*C. bancanus*) have been often described as "bird-like", referring to their similarities with birdsongs (Crompton & Andau 1987), but more details are lacking. Thus, to our knowledge, 85.7 % of Tarsiidae species emit songs (12 species out of 14). Future investigations on Philippine tarsier (*C. syrichta*) vocal behavior would clarify if this value will rise to 92.8%, possibly questioning the singularity of the non-singing behavior in the Horsefield's tarsier (*C. bancanus*). In contrast to duet, reports of solos are only anecdotal, and the occurrence of this particular case of singing behavior has not been extensively investigated. We found mention of solos in only two species (Tab. SM1), while duets in pygmy tarsier (*T. pumilus)* consist of "any call, where the male and female vocalize in synchrony" (Grow 2019). Even if there are indications that, in gen. *Tarsius*, all adults, and some sub-adults can join the duet song of the pair, creating a family chorus (Groves & Shekelle 2010; Gursky 2015), we found reports of chorusing behavior only on 35.7% (5 species out of 14) of the Tarsiidae.

Tarsiers show considerable variation in social structure. This family has different social/mating systems comprising genetic monogamy, pair-bonds with facultative polygyny, and *noyau*/dispersed polygyny. The mating system of some species remains unclear, but their social system has been described as comprising multi-males and multi-females groups (Tab. SM1).

Finally, tarsiers are considered territorial, although most of the evidence seems to rely on qualitative rather than quantitative data, such as the idea that duets are emitted for territorial advertisement (MacKinnon & MacKinnon 1980) and scent marking behavior (Gursky-Doyen 2010). Thus, we found indications of territorial behavior for 57.1% of species (8 out of 14).

Indris. Its distinctive black and white pelage and its loud song make indri (*I. indri*) one of Madagascar's best-known lemur species. Indris are diurnal, arboreal, and mostly folivorous (Powzyk & Mowry 2003). The indris' song is a long sequence of vocal units organized in phrases (Gamba et al. 2011; De Gregorio et al. *in press*). The song can be uttered by two (a duet) or more individuals (a chorus - Tab. SM2). Duet songs can occur between members of the pair or between one pair member and an offspring of the opposite sex (Gamba et al. 2016). Floating solitary individuals, that range unassociated with other reproductively mature individuals, rarely perform solo song bouts (Gamba et al. 2016). The family groups are composed of the adult pair and their offspring and contain two to six individuals (Torti et al. 2013). Despite the observation of an extra-pair copulation (Bonadonna et al. 2014), genetic monogamy is the norm (Bonadonna et al. 2019). Family units occupy relatively small territories that are stable in terms of size and location, with core areas that remain stable over the years (Bonadonna et al. 2020). Intergroup encounters are rare and are frequently mediated by prolonged vocal interactions given by all family members, also indicated as territorial songs (Torti et al. 2013).

Gibbons. The family Hylobatidae is the only member of the Catarrhine monkeys showing singing behavior. They are medium-sized primates, arboreal, and mostly frugivorous. According to the latest gibbons' phylogeny (Shi & Yang 2018), this family includes four genera: *Hylobates*, *Nomascus*, *Hoolock*, *Symphalangus*. Following the classification proposed by Roos (2016), we considered the family Hylobatidae as composed of 20 species. All gibbon species emit songs. Duet represents the most widespread form of song organization (Fig. SM1D) and nearly all species have been reported to perform singing vocal interaction, corresponding to the 95% (19 out of 20) of the Hylobatids (Tab. SM3). Duets have been reported to occur mainly between the mated pair, but duetting between mother and daughter (*song matching duets*) can take place (Koda et al. 2013), and, occasionally, vocal interactions between mother and son have also been described, that can be considered as duet songs (Konrad & Geissmann 2006). Comparably to duets, direct evidence of solos is present for 95% of the total (19 species out of 20, Tab. SM3). In 40.0% (8 species out of 20) of the cases, both sexes have been reported to emit solos, while for 57.9% (11 species out of 20) only males. On the other hand, chorusing behavior has been reported in 50% of the species (10 out of 20), and in most cases, authors roughly reported the participation of the juveniles in the adults' duet (Tab. SM3).

Although gibbons are largely considered territorial primates (Bartlett 2009), we found direct indications of territoriality only in 60% of species (12 out of 20, Tab. SM3). For others, it is not clear to what extent the territory the familiar groups occupy is exclusive or not (Fei et al. 2012). Besides territoriality, monogamy has also been considered a common trait of this family. Nevertheless, we found a notable variability in social systems. Recent evidence suggests that the mating system in gibbons is not fixed and uniformly distributed as previously considered but comprises monogamy, polygyny, and polyandry (Tab. SM3).

Titi monkeys. Titi monkeys are primates of small/medium-sized living only in South America, mainly folivorous and found in various forest types. They belong to the subfamily Callicebinae, including three genera: *Callicebus*, *Cheracebus*, and *Plecturocebus* (Byrne et al. 2016), with 35 species in total (Gusmão 2019; Boubli 2019). Information about Callicebinae's vocal behavior is lacking (Adret et al. 2018). Authors often refer to song presence and features in the titi group as a whole, but when looking at the specific evidence, we found few studies actually describing song structure and organizations (e.g., Adret et al. 2018). 48.6% of titis (17 species out of 35) have been reported to perform duets (Tab. SM4; Fig. SM1E). There is descriptive evidence for solos (20 %, 7 species out of 35), and the frequency of this behavior is poorly known. The pair and its offspring emitted choruses only in 17.4 % of species (6 out of 35, Tab. SM4). Titis are considered genetically monogamous and pair-living (Fuentes 1998), but at the species level, we found indications on social systems only for 28.6% of them (10 out of 35). Likewise, to our knowledge, territoriality has been proven for 25.7% of them (9 species out of 35), and only in one case the evidence is mixed (Tab. SM4).

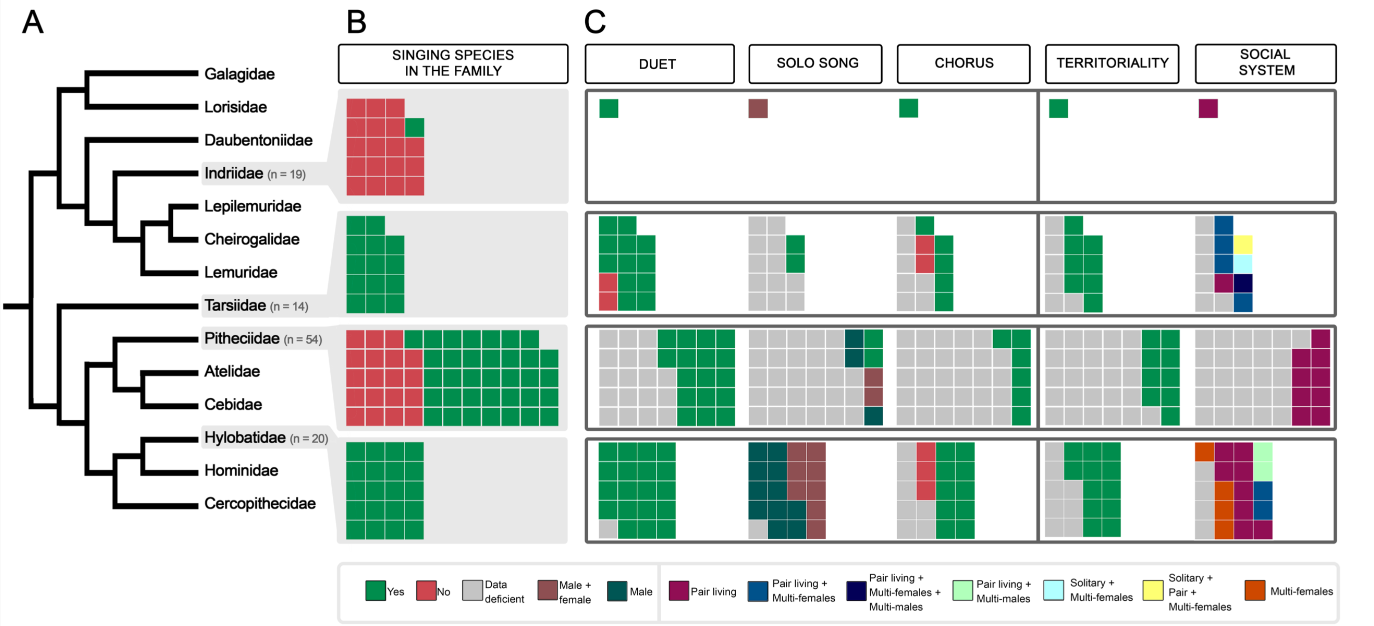

Fig.1. Schematic representation of the primates' singing behavior and characteristics. A. Phylogenetic relationship between primates' families historically considered as containing singing species. The families presenting singing behavior are highlighted in grey. B. Occurrence of singing species in each primates' family. Each square represents a species among a given family. C. Overview of the presence/absence of different song types and territorial behavior, and the type of social organization in the singing species. Singing species are represented by green squares from panel B.

Discussion

This work aimed to provide an overview of current knowledge about the co-occurrence of song, territoriality, and a pair-living social system in those primate taxa that historically have been considered showing singing behavior, as these traits have been linked to one another. Singing primates groups have often been presented as being uniform in their vocal activity and social/mating system. Nevertheless, we found descriptions of singing behavior only in 70% of singing primates' species (49 species out of 70; Fig.1C). For this reason, further considerations on the occurrence of different song organizations in singing primates' taxa will be based on 49 species. Several studies often refer to the emission of songs without providing explicit references or further details. We found the same for territorial behavior and social system: while many articles describe these animals as monogamous and territorial, in many cases, we found no work providing empirical evidence for the presence of these two behavioral traits. As pointed out by Fernandez-Duque et al. (2020), this might be due to the habit of referring to studies of historical value, but that may have less importance in the light of current research, especially when considering the critical changes in primate phylogeny. In fact, it is not obvious that newly described species possess the same ecological features of the group they have been separated from.

Many singing primates' social and mating systems are still unclear, and we did not find direct information for 51.4% of them (36 out of 70, Fig.1C). Thus, for our comparisons, we focused our attention on their social system and avoided mixing different social traits often grouped under the concept of "monogamy" (Fernandez-Duque et al. 2020). In particular, although many species for which it was possible to find the information (34 out of 70) presented mixed social systems, we found indications of pair-living in 85.3% of them (29 out of 34). Still, despite being a strongly present trait, we found that pair-living is not the rule for this taxon. In fact, 44.1% (15 out of 34) of the species presented multi-females/multi-males groups, in addition to pair-living (Tab. SM1), or even as primary social systems (Tab. SM3).

This aspect is fascinating, not only because it suggests that the strong link between singing behavior and a pair-living social system does not hold so firmly anymore, but also for what concerns song emission and duetting behavior. One might ask how singing behavior is regulated in polygynous or polyandrous species. To our knowledge, no studies have considered this aspect in singing primates. One speculation, for example, would be that, in polygynous species, duets would be emitted more frequently between the male and the higher-ranking female, if singing behavior advertises bonding (Geissmann 1999).

Concerning the territorial behavior, even if we found information only in 42.9% of species (30 out of 70, Fig. 1C), it is worth noting that all cases suggested the presence of territoriality. Only for the Atlantic tit (*Callicebus personatus* - fam. Pitheciidae), we found mixed evidence on both presence/absence of this trait (Price & Piedade 2001; Tab. SM4). Thus, in the light of the recent phylogenetic revisions of singing primates' taxa, we can conclude that territoriality seems to be more conserved than the social system. While the association between a monogamous social lifestyle and territorial behavior still holds for titi monkeys (Pitheciidae) and indris (Indriidae), we indeed found indications of multi-females and multi-males groups for gibbons and tarsiers.

Our work indicates that the duet is the most widespread among the different types of song organization, as it occurs in, at least, 70% of the species (49 out of 70). In particular, we point out that, following the most used definitions of duet song, species considered non-duetting might indeed be duetting. In fact, in this category, we also considered the *song matching duets* given by gibbons' species typically considered non-duetting: while duets between paired individuals do not occur (Geissmann 2002), singing interaction between mothers and daughters can indeed take place. Besides duets, we found information about chorusing behavior only for 27 species out of 70. Still, 22 species presented chorus songs (81.5%), and we are confident that, given that we could not find evidence for chorus songs for some singing primates living in family groups, future studies will find more information regarding this behavior. Finally, we found mention of solo songs only for 41.4% of singing primates (29 out of 70), often only as anecdotes.

It is quite clear that the study of solos and choruses in singing primates is still in its descriptive phase. Future studies will elucidate if these are infrequent displays or if the scarcity of their reports may be due to the complexity of studying animals in the wild, which raises a wide range of difficulties concerning the intrinsic nature of their habitats and the need for long habituation periods (Pinto et al. 2013). Here, we reported the occurrence of different song organizations in various singing primates' groups. The current scarcity of data limits our clear understanding on how these different behavioral traits have evolved in these fascinating animals. More information will be needed to understand which ecological conditions favored the presence of a particular song organization over another in a given species. It is also possible that stepping away from the idea of a pair-living social system as a rule, and starting to consider the variety of social systems in these taxa, will be a helpful approach to disentangle the selective pressures that led to the emergence and organization of singing behavior.

AUTHOR CONTRIBUTION

C. De Gregorio: conception of the work idea. C. De Gregorio, F. Carugati, D. Valente, T. Raimondi. V. Torti and L. Miaretsoa: literature research and organization of information. T. Raimondi: visualization. M. Gamba and C. Giacoma: critical revision. All authors contributed to the final version of the manuscript.

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