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This is the author's manuscript

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1736938 since 2022-01-24T10:01:20Z

Publisher:

Ravignani A., Barbieri C., Flaherty M., Jadoul Y., Lattenkamp E., Little A., Martins M., Mudd K., Verhoef T.

Published version:

DOI:10.17617/2.3190925

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10 September 2026

SEXUAL DIMORPHIC CHORUSING IN THE WILD INDRIS

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Animals can produce vocal rhythms in an interactive, coordinated manner (Couzin 2018). Comparing structural, spectral and temporal features across species (Fitch 2000) may help in reconstructing the evolutionary history of human speech (Ravignani and Norton 2017). Singing primates (Geissmann, 2000), which produce elaborated and complex sequences of vocalizations, are of particular interest for this topic. Similarly to humans, indris (*Indri indri*) assemble simple units into more complex structures to convey different information. Individuals react differently to different songs, confirming the presence of functionally referential communication systems (Clark et al. 2006).

Indris are the only singing lemurs and emit songs whose most distinctive portions are "descending phrases", made of 2-5 units. Mated indris have been reported to sing in pairs, to enhance pair-bonding and defend their territories (Pollock, 1986; Torti et al., 2013; Bonadonna et al., 2017). Songs may have the form of a chorus whenever the subadult members of the groups also utter their contribution in a precise and coordinated manner (Torti et al., 2018). Indri songs exhibit turn-taking between individuals of different sexes and a variable degree of overlap between group members (Gamba et al., 2016). Songs have various functions depending on the context in which are emitted (Torti et al., 2013), and they are used for both inter and intra-group communication.

We recorded spontaneous vocalizations of 8 groups of indris at the Maromizaha New Protected Area (18°56′S, 48°27′E), from 2008 to 2018. Focal animal sampling (Altmann, 1974) allowed the attribution of each vocal profile to a signaler. To investigate the timing and rhythm of songs, we measured the amount of co-singing between different individual contributions (percentage of overlap;

Gamba et al. 2014) and the inter onset intervals (IOIs, duration between the starting points of two successive notes in the same song; Gamba et al. 2016) of adjacent units (Sasahara et al., 2015). We extracted the pitch contour and labeled each unit using the phrase in which it was emitted and the sex of the emitter. We then calculated the similarity across different individual songs using the Levenshtein distance. Finally, we classified song units in phrases through DTW and clustering analyses (Gamba et al. 2018).

Our results show that: a) indris can synchronize their utterances showing non-random overlap between singers, with an overlapping rate of the pair contributions that changes according to the number of singers in the chorus; b) both dominant and non-dominant indris can coordinate their calls and there is evidence for an ability of precise timing during song emission; c) indri songs show the presence of sex dimorphism, both in the overall timing and repertoire size than in the unit and phrase structure, with females being more flexible than males in their contributions, and d) the structure of phrases possess individually distinctive characteristics.

In line with previous findings (De Gregorio et al., 2018), we observed that indris within a group coordinate on average more than 70% of their contributions suggesting that duetting is indeed associated with pair cohesion, as a proxy of the strength of the pair bond (Geissmann & Orgeldinger, 2000). The most consistent portion of the song, made of ascending or descending sequences of units, shows reliable timing and pitch variation, a crucial feature of birdsong and human speech (Levinson & Holler, 2014). We found support for our prediction that the phrase structure of songs varied between reproductive males and females. The presence of pitch sex dimorphism in nonhuman primate vocal signals is rare and is identified as a prerequisite in the evolution of human perceptual abilities (Patel, 2010). It appears that indri male's song has a more fixed pattern, whereas females could adjust their contribution, in agreement with findings on the white-cheeked gibbons N. leucogenys (Deputte, 1982), on baboons and Japanese macaques (Lemasson et al., 2011; Lemasson et al., 2016). Our results also show that strong individuality is encoded in the indris' phrases, thus the potential to provide conspecifics with emitter's identity cues.

Studies on rhythm and synchrony in primates have historically been focused on anthropoid species (Ravignani, 2019), with poor investigation on prosimian vocal behavior. Our study suggests that the indris are a good model for further investigations of the evolution of human speech features, because of the turn-taking between individuals and the variable degree of overlap, commonly identified as traits of modern human communication.

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