

Article

Evidence for acoustic discrimination in lemurs: a playback study on wild indris (*Indri indri*)

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Abstract

Indris *Indri indri* are group-living lemurs that occupy stable territories over several years and perform remarkable long-distance vocal displays. Vocal exchanges between long-term territory neighbors may contribute to assessing reciprocal resource-holding potentials, thus adaptively reducing the costs of territorial defense by limiting aggressive escalation. Previous work showed that indris' songs show distinctive acoustic features at individual and group level. However, the possibility that indris use such cues for individual or group-level recognition has never been investigated experimentally. We conducted a playback experiment to test whether indris discriminate between familiar and unfamiliar songs. Our rationale lies in the hypothesis of the dear enemy phenomenon, which predicts that territorial animals will show reduced aggression levels toward familiar neighbors compared with novel rivals. We played back stimulus recordings to wild indris from their territory boundaries and examined their responses in terms of vocal and behavioral indicators of willingness to engage in a fight. In line with our predictions, focal animals responded more rapidly and approached more often the speaker in response to playback stimuli of unfamiliar individuals than to stimuli of neighboring groups. These results indicate that indris can discriminate between different classes of intruders based on distinctive acoustic features of their song choruses. We suggest that increased aggression directed toward unfamiliar intruders may be explained by higher threat levels associated with dispersal and group formation dynamics. We further discuss the relevance of these findings in a strepsirrhine primate model for comparative studies of vocal communication and sociality.

Key words: acoustic communication, dear-enemy effect, neighbor–stranger discrimination, primate communication, song, territoriality.

The ability of territorial animals to discriminate among surrounding competitors is instrumental in adaptively regulating aggressive interactions (Christensen and Radford 2018). Across taxa, territory owners often show reduced aggression toward long-term neighbors as compared with unknown or unusual (e.g., distant) rivals, so that the former are referred to as “dear enemies” (Fisher 1954). Two

hypotheses have been put forward to explain this phenomenon. The *familiarity* hypothesis posits that intrusions from dear enemies are responded to less vigorously since long-term acquaintance allows a more efficient assessment of reciprocal resource-holding potentials (Ydenberg et al. 1988), or because familiar opponents have nothing more to learn about each other, assuming a “fighting to learn”

rationale (Getty 1987). Alternatively, the *threat level* hypothesis predicts responses to intrusions to be proportionate to the threat posed by the intruder (Temeles 1994). For instance, unfamiliar rivals (e.g., floaters or newly formed groups) often usurp larger parts of the territory compared with neighbors in some species (e.g., Radford 2005) and may additionally reduce the reproductive fitness of territory owners via sexual harassment or extra-pair copulations. On the contrary, neighbors only jeopardize exclusive sexual access to the owner's partner—as they already possess a territory (Temeles 1994).

Indeed, long-term familiarity with neighbors has been shown to produce positive fitness consequences, for example by increasing survival (Seppä et al. 2001; Beecher et al., 2020), enhancing overall condition (Liebgold and Cabe 2008) and affecting reproductive success (Beletsky and Orians 1989; Grabowska-Zhang et al. 2012). From the perspective of the proximate mechanisms, dear-enemy dynamics can therefore be interpreted as a mutually altruistic relationship, where re-negotiations of territory borders are resolved inexpensively for both groups and individuals. Yet, game theory predicts that for dear-enemy (mutualistic) tactics to be evolutionarily stable, cheaters must suffer retaliation (Getty 1987; Godard 1993; Krams et al. 2008). Territory owners should thus respond vigorously to any disruption in their usual social environment, which may challenge negotiated boundaries. Along with intrusions from stranger invaders, this detrimental effect can also be exerted by unruly versus cooperative neighbors. It has been shown that some territorial animals retaliate against defecting neighbors (Dalton et al. 2020) and can discriminate the more aggressive ones among their neighbors (Hyman and Hughes 2006) or those who have cheated before (Stoddard et al. 1991; Akçay et al. 2009, 2010), based on their identity.

Scanning the social environment and determining the identity of an upcoming intruder requires refined discrimination abilities. Neighbor–stranger discrimination is defined as the ability to recognize and respond differently to conspecifics based on individual signatures in their signal type or structure (Brooks and Falls 1975; Stoddard et al. 1990; Radford 2005; see also Carlson et al. 2020). A variety of signal types can convey information about emitter identity and provide the potential for both neighbor–stranger discrimination and the associated dear-enemy dynamics. In some habitats, vocal communication offers a more effective channel for signal transmission, as compared with olfactory or visual signals. Long-carrying acoustic properties of loud calls have been shaped by evolution to overcome ecological constraints in forest habitats such that these signals can be efficiently addressed to a remote receiver (Haimoff 1986). The adaptive value of such loud calls during territorial interactions and the underlying discrimination skills have been investigated in a variety of taxa, with a particular focus on territorial birds (Becker 1982; Temeles 1994; Akçay et al. 2009; Radford 2005; Olendorf et al. 2004; Hyman 2002; Benteen et al. 2020; Ferrandiz-Rovira et al. 2020; reviewed in Christensen and Radford 2018).

In primates, vocal discrimination and/or the associated dear-enemy dynamics have been investigated in some territorial species [mangabeys (Waser 1977), vervet monkeys (Cheney and Seyfarth 1982), spider monkeys (Teixidor and Byrne 1997), gibbons (Ham et al. 2016; Raemaekers and Raemaekers, 1985; Mitani 1985, 1987; Wich et al. 2002), and chimpanzees (Herbinger et al. 2009)]. A number of species were shown to also adjust territorial responses based on acoustic numerical assessment of the opponent's group size (Wilson et al. 2001; Kitchen 2004; Meunier et al. 2012). Interestingly, primates with fission–fusion social organization exhibiting low territoriality show stronger responses toward calls from own group members, and do not seem to discriminate the identity of external groups or individuals (Bergman 2010; Maciej et al.

2013), either because they are not motivated or unable to do so (Maciej et al. 2013). Despite increasing interest in cognition and communication in Strepsirrhini primates (i.e., lemurs and lorises) (Fichtel and Kappeler 2010; Kitterler et al. 2015; Norscia and Palagi 2016), group-level vocal discrimination has never been investigated in this clade [Oda 2002; Baker-Medard et al. 2013; but see Kessler et al. (2018) and Génin (2021) for playback studies in Strepsirrhini primates]. Addressing this question in Strepsirrhini primates is essential for shedding light on the origin of communication systems in the Primate order. In particular, the ability to extract and use social information in lemurs may help understand the link between communication and social systems in this clade.

Indris *Indri indri* are group-living lemurs that hold stable occupancy of territory for several years. This species is best renowned for its remarkable vocal repertoire, which includes a sequence of powerful modulated notes ranging 0.5–1.7 kHz in fundamental frequency (Thalmann et al. 1993; Gamba et al. 2016), known as the indri song (Supplementary Figure S1). The dominant pair within the family group performs song duets and choruses, together with other adult and sub-adult individuals (Pollock 1986; Torti et al. 2018; De Gregorio et al. 2019). Advertisement of territory occupancy was pointed out as the most prominent functional explanation for this display, although group cohesion is also involved (Torti et al. 2010, 2013). Moreover, one chorus usually elicits other indri groups' replies contagiously (Pollock 1975; Powzyk and Thalmann 2004). Among lemurs, indris are ideal candidates for investigating vocal discrimination abilities related to territorial dynamics. First of all, regular vocal contact is maintained through intergroup vocal exchanges. Along with vocal interactions, indri groups occasionally confront neighbors in physical disputes, during which territory boundaries are re-negotiated (Bonadonna et al. 2017, 2020) and reciprocal resource-holding potentials are assessed (Pollock 1975, 1986). Moreover, long-termed relationships are likely to exist locally among confining family groups. Second, previous studies have shown individual- and sex-specific differences in temporal and frequency parameters of indri songs (Giacoma et al. 2010; Baker-Medard et al. 2013; Zanolini et al. 2020), which may therefore convey information about the caller's identity and sex, and provide potential for neighbor–stranger discrimination. One may thus expect each group to keep track of the surrounding social environment via acoustic discrimination abilities, although this possibility has never been experimentally investigated (Baker-Medard et al. 2013). Finally, newly formed dispersing groups (along with individually dispersing animals) have been observed in this species (Bonadonna et al. 2020). Although our knowledge on dispersing distances and group formation dynamics in indris is limited, anecdotal reports suggest that territory eviction and/or sexual interference by unfamiliar roaming animals may indeed occur. Thus, while encounters with familiar neighbors commonly result in the re-negotiation of established territory boundaries, intrusions from unusual, dispersing rivals may pose a greater threat in terms of both territory takeover and sexual competition (see above). We hypothesize that vocal discrimination skills in indris should thus adaptively benefit territory owners in identifying the relative costs and threat levels associated with specific social encounters.

In this study, we investigated the adaptive value of the indri song as a device that regulates territory defense. Our aim is to enquire into discrimination skills and dear-enemy dynamics in a population of wild indris. As intergroup encounters in this species are relatively rare in the wild (Bonadonna et al. 2017), we conducted a manipulative playback experiment to simulate interactions with familiar neighbors and unusual intruders, namely distant and unfamiliar groups. We played back stimulus recordings from the limit of each group's territory and noted the

animals' reactions in terms of vocal and behavioral indicators of willingness to engage in a fight. We predicted that: 1) indri groups should react less vigorously toward playback calls from familiar neighbors as opposed to unfamiliar groups; 2) playback trials conducted during the breeding season should elicit stronger responses, due to increased threat levels via sexual competition; and 3) numerical assessment of group size in the stimulus songs should also exert an effect on response magnitude.

Materials and Methods

Study site and study animals

This study was conducted in the Maromizaha New Protected Area (NAP), a moist evergreen mid-altitude forest located in the Moramanga District, central-eastern Madagascar (18° 56' 49"S—48° 27' 53"E). The area ranges 800–1,200 m in altitude (Hervieu 1960; Randrianarison et al. 2015) and covers 2,150 ha in the surface. The climate is temperate humid, with annual mean rainfall ranging 1,500–2,000 mm and peaking in January and December (Pollock 1975); monthly mean temperatures vary between 15.4°C in June and July and 21.4°C in February (Randrianarison 2019). Study animals are part of a population with a long-term record of behavioral and spatial observations. Sex, group membership, social, and dominance status of each individual within a group are based on previous observations conducted since 2008. Territory boundaries are known via GPS data collected for each group since 2009 and updated each year before the experimental sessions. For instance, average territory size in three indri groups in the Maromizaha NAP ranged from 9.7 to 15.1 ha between 2009 and 2014 (Bonadonna et al. 2020).

Playback stimuli

All playback tracks were naturally occurring advertisement choruses recorded in the wild from ~20 m from the caller groups, with a sampling rate of 44,100 Hz. “Neighbor” stimuli were recordings from local groups that shared territory boundaries with each given test group. “Non-neighbor” stimuli were songs recordings from indri groups that did not have a history of direct interactions with the experimental groups. We recorded these latter stimuli in 4 different forest sites (distances from Maromizaha Forest: Anjozorobe-Angavo = 68 km; Mitsinjo Station Forestière = 7 km; Analamazaotra Special Reserve = 5 km; Mantadia = 16 km) and from distant non-neighboring groups from the same site (e.g., whose territory boundaries were not shared with each of the experimental groups). In this latter case, our subject animals may have previously heard stimulus songs—as territories are smaller than song carrying capacity (unpublished data). We recorded neighbor and non-neighbor groups multiple times and used different recordings for each trial on the same subject group. To avoid pseudoreplication (Kroodsma 1989; Kroodsma et al. 2001), different stimulus tracks were used across trials. We broadcast a total of 89 playback stimuli of standardized duration of 3 min, using a MOVE 60 RCF loudspeaker; output volume was standardized to reach 105 dB of intensity at the source.

Data collection

Playback trials were conducted on nine focus groups during 4 years of data collection—between October 2012 and September 2016. We conducted playback experiments in the morning hours (6 a.m. to 12 p.m.) when animals were stationary, that is when feeding or resting (Ham et al. 2016), and during favorable weather conditions, as adverse weather affects singing behavior and the probability that advertisement songs from one group are responded to by other groups (unpublished

data, but see also Clink et al. 2020). If song choruses had already started in the study site prior to a testing session, playback stimuli were broadcast after a delay of at least 1 h since the test group or any other group in the study area last sang. We broadcast stimulus songs when a given focal group was in proximity to territorial boundaries, that is, at an approximate distance of 50–100 m from known territory boundaries based on long-term data (Bonadonna et al. 2017). The playback apparatus was concealed and placed at ground level just outside the territory boundary (see Stoddard et al. 1990), at a distance of ~100 m from the focal group. We played back neighbor songs from the correct territory border of the corresponding stimulus group (i.e., the usual direction from which naturally occurring songs from those groups are heard), whereas we broadcast non-neighbor stimuli from a suitable territorial boundary, depending on the position of the focal group in relation to other adjacent territories.

We conducted a total of 89 trials, 51 of which simulating neighbor songs and 38 simulating non-neighbor songs. Each group was tested 9.89 ± 10.16 times (mean \pm SD) (range: 2–30 trials). Our ability to conduct the same number of replicates on all experimental groups was affected by field limitations and was further limited by the correct positioning of the focal group with respect to their territory border. Reply songs from subject groups were recorded at a distance of ~20 m using a Tascam DR-100MKII 24 bit/96 kHz Linear PCM digital recorder, with a sampling rate of 44,100 Hz. Neighboring groups never approached the sites of the experiments during playback trials, and playback stimuli elicited song choruses in groups other than the focal group in 4.5% ($N = 4$) of the trials. The focal groups were followed for at least 1 h before the experiment started and behavioral responses for each group member were noted before and after the onset of the playback by 2 or 3 observers who were blind to the type of stimulus being broadcast; 2 observers stood next to the speaker. We considered the following response variables as indicators of “readiness of the defenders to engage in a contest” (sensu McComb et al. 1994): 1) whether or not the animals called back to the stimulus (0 = no reply song; 1 = reply song), 2) whether or not the reply song overlapped the stimulus song (0 = no overlap; 1 = overlap), 3) the latency to respond in seconds (time measured from the onset of the recording), 4) the duration of the reply song in seconds, 5) whether or not the animals approached the source of the stimulus (0 = no approach; 1 = approach), 6) occurrence of cheek and/or anogenital marking within 15 min from the onset of the recording (1 = presence of marking, 0 = absence of marking), and 7) utterance of “kiss” and/or “kiss-wheeze” vocalizations (within 15 min from the onset of the recording (1 = presence of vocalization, 0 = absence of vocalization). Kiss and kiss-wheeze vocalizations are uttered in stress-related contexts and during agonistic interactions (Maretti et al. 2010). The latter 4 behavioral responses were only analyzed for the adult couple, as behaviors of juvenile and sub-adult family members during intergroup contests occasionally proved to be ambiguous.

Data analysis

To detect possible effects of playback condition on our 7 vocal and behavioral response variables, we used generalized linear mixed models (GLMMs), running separate models for each variable using *lme4* package in version R 3.6.2 (R Core Team 2015). We used the function *lmer* for continuous response variables and *glmer* for binary response variables, for example, overlap (0 = no overlap; 1 = overlap). We included the following predictors as fixed effects in each model: 1) playback type (neighbor versus non-neighbor treatment), 2) season (summer versus winter), and 3) the number of callers in the playback stimulus. To test whether the number of singers in the subject group positively affects reply song duration and

latency, as suggested by previous observations (Pollock 1975; Torti et al. 2018), we also included number of singers in the subject group for each trial as a fixed effect in the model for reply song duration and latency. Due to limitations during data collection (e.g., visibility of the animals, quality of audio recordings), we excluded for each response variable those trials for which data were missing. For example, instances of incomplete data about individual animals within a group are due to occasional sudden group responses, such as abrupt rushes toward the playback source, and the ensuing loss of focal individuals through thick vegetation. As a result of these limitations, the number of trials varies between models (see below).

Finally, as different stimuli from the same neighbor and stranger groups were used in subsequent replicates, we statistically controlled for group identity by including random effects for stimulus group. To control for group-specific reactions to playback stimuli, random intercepts were also included for the identity of the test groups. No random slopes were theoretically identifiable due to little variation of the fixed effects within the levels of the random effects, thus we used a mixed model approach with random intercepts without including random slopes (Schielzeth and Forstmeier 2009; Barr 2013).

To verify the assumptions that residuals are homogeneous and normally distributed, we inspected qqplots, and the distribution of the residuals plotted against fitted values. Using the function *vif* of the *car* package, we obtained variance inflation factors (Field 2005) values for each predictor variable, using 4 as a threshold value, thus excluding the possibility of collinearity among predictors (O'Brien 2007). We compared the full model to a null model using a likelihood ratio test (Anova test with argument "Chisq"; Dobson 2002), to assess the significance of the former (Forstmeier and Schielzeth 2011). The null model lacked the test predictors and only included the same random effects as the full model. *P*-values were then

calculated using the function *drop1* (Barr 2013). For the full models showing significant differences compared with the null models, we assessed model stability by excluding random effects one at a time and comparing the obtained estimates with those from the model based on the full data (Nieuwenhuis et al. 2012). Our models showed good stability except for the "approach" model, particularly for our test variable "playback type" (see Results section). We calculated confidence intervals (CIs) using the function *bootMer* of the package *lme4*, using 1,000 parametric bootstraps. Effect sizes were determined using the function *r.squaredGLMM* of the package *MuMIn* (Nakagawa et al. 2017; version 1.43.6; Barton 2018).

Results

Subject groups responded to the playback input signals in 58 out of 89 trials. The full model for the response variable "response to playback stimulus" (0 = no response; 1 = response; $N = 89$) did not differ significantly from the null model (response to playback: $\chi^2 = 1.38$, $df = 3$, $P = 0.711$). None of the predictors had an effect on the probability of a group to respond to a playback track. The duration of reply songs averaged 96.95 s ($N = 53$; $SD = 33.63$ s). The full model for song duration ($N = 53$) fit significantly better than the null model (full versus null: $\chi^2 = 25.361$, $df = 4$, $P \leq 0.001$). The number of singers had a significant effect on reply song duration ($P \leq 0.001$) (See Song duration in Table 1; Figure 1).

The stimulus song was overlapped in 36 out of 56 trials. The full model for the overlap ($N = 56$) fitted significantly better than the null model ($\chi^2 = 11.093$, $df = 3$, $P = 0.011$). The season in which the trial was conducted had a significant effect on the probability of overlapping the stimulus song (See Overlap in Table 1). More specifically, stimulus songs were more frequently overlapped during "summer" trials.

Table 1. Results of 4 models showing for each response variable the effects of playback type (neighbor versus non-neighbor), season (winter versus summer), number of singers in a reply song, number of callers in a playback stimulus, and sex (in the approach model only)

Variable	Estimate	SE	df	χ^2	<i>P</i>	Lower CI	Upper CI
1. Latency							
Intercept	4.480	0.717	NA	NA	NA	2.480	5.860
Playback type	-0.944	0.289	1	9.333	0.002	-1.549	-0.341
Season	-0.014	0.248	1	0.003	0.957	-0.524	0.473
Number of singers	0.127	0.196	1	0.403	0.526	-0.271	0.561
Number of callers	-0.088	0.198	1	0.172	0.679	-0.488	0.310
2. Song duration							
Intercept	3.684	0.203	NA	NA	NA	3.297	4.090
Playback type	-0.041	0.068	1	0.361	0.548	-0.182	0.105
Season	-0.100	0.066	1	2.237	0.135	-0.239	0.042
Number of singers	0.277	0.052	1	22.874	<0.001	0.170	0.376
Number of callers	0.057	0.057	1	1.005	0.316	-0.057	0.158
3. Approach							
Intercept	-0.940	1.313	NA	NA	NA	-3.849	1.797
Playback type	1.545	0.602	1	8.584	0.003	0.457	2.976
Season	-0.174	0.441	1	0.154	0.694	-1.242	0.796
Sex	0.266	0.373	1	0.508	0.476	-0.479	1.219
Number of callers	-0.133	0.410	1	0.103	0.748	-1.132	0.789
4. Overlap							
Intercept	1.027	1.687	NA	NA	NA	-2.998	14.966
Playback type	0.971	0.777	1	1.621	0.203	-15.308	-1.042
Season	-2.435	0.943	1	9.991	0.002	-0.626	3.592
Number of callers	0.230	0.618	1	0.141	0.708	-1.322	2.229

Neighbor is the reference category for Playback type; *Summer* is the reference category for Season; *Female* is the reference category for Sex; SE, standard error; *P*-value significance level $P \leq 0.050$, significant *P*-values in bold; lower and upper 95% CIs; NA not reported as having limited interpretation.

When indris responded to a playback track, the latency to start the reply song averaged 82.29s from the onset of the stimulus ($N=47$; $SD=62.11$ s). The full model for latency ($N=47$) had a significantly better fit than the null model ($\chi^2=10.495$, $df=4$, $P=0.032$). The latency to respond to “non-neighbor” stimuli was significantly shorter than the response latency to “neighbor” stimuli. (see Latency in Table 1; Figure 2A). The full model for the approach response ($N=141$, including both males and females) fit significantly better than the null model ($\chi^2=10.710$, $df=4$, $P=0.030$). Playback type had a significant effect on the response variable (see Approach in Table 1). More specifically, the probability of approach to the stimulus song was higher for “non-neighbor” stimuli (Figure 2B). The full model for the 2 other behavioral responses

(probability of uttering an alarm vocalization and of anogenital marking) did not fit significantly better than the relative null models (anogenital marking: $\chi^2=8.67$, $df=4$, $P=0.069$; vocalization: $\chi^2=7.18$, $df=4$, $P=0.126$).

Discussion

This study presents novel experimental evidence of acoustic discrimination in lemurs, in agreement with previous findings in territorial monkeys (Waser 1977; Cheney and Seyfarth 1982; Teixidor and Byrne 1997) and apes (Herbinger et al. 2009). Moreover, our results align with the predictions of the dear-enemy hypothesis, adding to the existing body of literature on territorial behavior in other primate taxa. In particular, we show that responses to neighbor versus non-neighbor stimuli varied significantly for 2 of our test variables. First, animals responded more rapidly to non-neighbor stimuli than neighbor stimuli (Figure 2A; see Latency in Table 1). A prompter reply was thus directed toward simulated intrusions from unfamiliar indris, similar to previous findings from playback studies in gibbons (Wich et al. 2002; Radford 2005; Ham et al. 2016). Second, the probability of indri groups to approach non-neighbor stimuli was higher than neighbor stimuli (Figure 2B; see Approach in Table 1). Approaching the source of a call was interpreted here as a proxy of evicting intentions and aggression (see Mitani 1984, 1985, 1987; Maciej et al. 2013), which again indicate higher aggression levels toward unfamiliar stimuli. These data on indris—the only singing lemurs—are, therefore, suggestive of vocal recognition and indicate that neighbor–stranger discrimination can be mediated by such unique signal type (Carlson et al. 2020).

Though lemurs have relatively smaller brains among other primate lineages (Dunbar and Shultz 2007; Isler et al. 2008), a growing body of literature shows that many of their cognitive abilities are similar to those of haplorrhine primates (i.e., monkeys and apes)

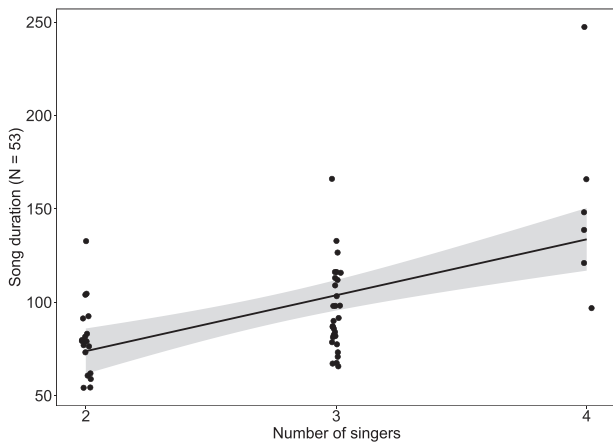


Figure 1. Duration of reply songs (in seconds) to playback stimuli as a function of the number of singing individuals. Depicted is the fitted model (black line) with the 95% CIs (gray shading).

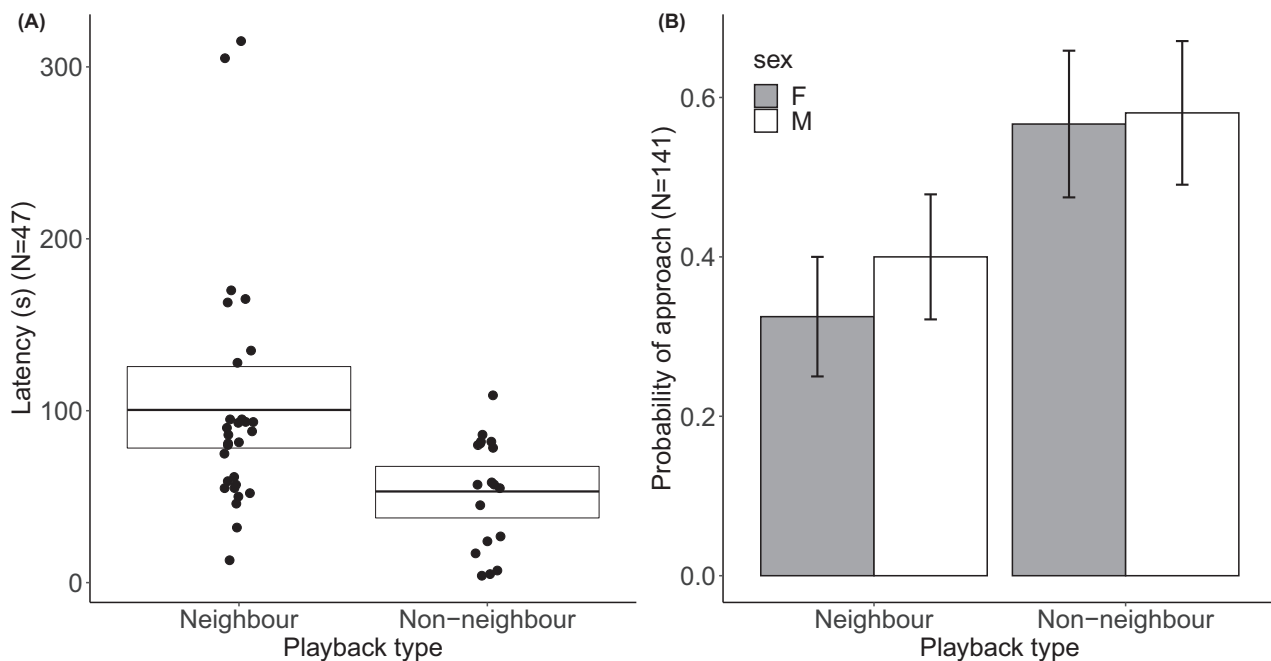


Figure 2. (A) Latency (in seconds) of subject groups to respond to playback stimuli plotted against playback type. Horizontal lines indicate the fitted model with the respective 95% CIs. (B) Proportions of playback stimuli ($\pm SE$) approached by the subject groups to the source of the stimulus. Proportions are shown separately for sex and playback type.

(e.g., Santos et al. 2005; Deppe et al. 2009; Fichtel and Kappeler 2010; Kittler et al. 2018). These data argue against “the existence of a possible deep behavioral and cognitive gap” (Fichtel and Kappeler 2010) between anthropoids, monkeys, and other non-human primates (see also Arbib et al. 2008; Norscia and Palagi 2016; Masters and Génin 2016; Fichtel et al. 2020). Evidence from studies on vocal communication can further contribute to filling this gap. For instance, referential signaling—an essential feature of human communication (e.g., Cheney and Seyfarth 2010; Sievers and Gruber 2016)—has been shown in ring-tailed lemurs *Lemur catta* (Macedonia 1990, 1993; Pereira and Macedonia 1991; see also Torti et al. 2010). Also, contact calls between mother and infant in gray mouse lemurs *Microcebus murinus* meet the criteria for vocal greeting displays and have been suggested to represent the evolutionary precursor of greeting behavior in humans (Scheumann et al. 2017). Our findings build on this growing body of literature by presenting evidence of vocal discrimination in lemurs. Taken together, these data are particularly valuable in that they may inform comparative studies aiming to investigate shared traits between strepsirrhine and haplorrhine primates (Fichtel and Kappeler 2010). In order to better understand the relationship between social structure, group size, and acoustic discrimination, future studies should focus on investigating discrimination in other group-living lemurs. Indeed, within the strepsirrhine suborder, lemurs are of particular interest in this respect, as group-living is only found within this clade, yet this trait is widespread in haplorrhine primates. Thus, though limited to one single species, our results provide novel information about social and communication systems in primates, and shared cognitive traits within the order (Oda 2001).

Previous work on the acoustic properties of indris' songs found distinctive individual (Baker-Medard et al. 2013; Torti et al. 2017) and sex (Giacoma et al. 2010; Gamba et al. 2016; Zanoli et al. 2020) signatures in both temporal and frequency song parameters (Baker-Medard et al. 2013; Gamba et al. 2016). Our study shows that such acoustic cues are used by indris to regulate territorial behavior at a group level and to inform decisions concerning agonistic responses to acoustic stimuli. Future studies could deploy artificial stimuli with modified temporal and frequency properties to investigate what specific acoustic parameters play a more prominent role in conveying information about group identity, or in eliciting territorial responses. For instance, temporal parameters—such as song duration—are linked to particular territorial contexts in this species. Indris emit specific songs (so-called “Territorial Songs,” Torti et al. 2013) during short-distance territorial encounters, that is, when vocal exchanges escalate to close-range disputes. Such territorial songs were shown to be longer in duration than common advertisement songs (Torti et al. 2013). Likewise, howler monkeys *Alouatta pigra* emit longer calls during intergroup encounters than do during spontaneous calls, indicating that song duration in this species is indeed linked to threat level (Sekulic and Chivers 1986; van Belle et al. 2013; but see Kitchen 2004). Nevertheless, we did not observe any variation between the 2 playback conditions regarding reply song duration in this study, and song duration was only affected by the number of singers participating in the reply song (Figure 1; see Song duration in Table 1). This result aligns with previous reports that advertisement song duration in indris is related to singers' number (Pollock 1975; Torti et al. 2018), as non-dominant family members tend to overlap less in the group chorus than the adult pair (Gamba et al. 2016), ultimately resulting in longer calls. Moreover, as only advertisement songs were used as playback stimuli in this study, this finding further suggests that indris may use a different code when

advertising territory ownership than when defending it from forthcoming intrusions (Torti et al. 2013). Hence, future studies should focus on simulating close-range territorial contests to investigate whether further differences in vocal and aggressive responses to different classes of intruders may emerge in such contexts.

According to our second prediction, we expected that responses to simulated intrusions would be more intense during the breeding season, corresponding in this species to the austral summer. We found that more playback songs were indeed overlapped during the austral summer (see Overlap in Table 1), suggesting that simulated social encounters during the breeding season elicited stronger responses, due to increased threat levels via sexual competition. Playback studies in other monogamous singing primates revealed that both territoriality and maintenance of monogamy are involved in the utterance of song duets, for example in gibbons (e.g., Cowlshaw 1992). The comparison with gibbons seems to be particularly informative, as these monogamous singing primates share with indris a number of ecological and life-history features. For example, Raemaekers and Raemaekers (1985) found evidence for sex-specific responses toward playback stimuli of different sexes in lar gibbons *Hylobates lar* (see also Mitani 1984, 1987). Group choruses may thus advertise both territory occupancy and pair-bonded state of the calling couple also in indris, as extra-pair copulation during the breeding season may severely impact reproductive fitness (Bonadonna et al. 2014), although responses to solo songs were not tested in this study. Overall, these results support our hypothesis that unlikely intruders (i.e., unfamiliar and distant territorial groups) may pose a greater threat to territory holders than familiar neighbors, in terms of both territory takeover and sexual competition. Although our knowledge about dispersal and territory forming dynamics in the species is limited, we can conjecture that newly formed or dispersing groups may jeopardize not only territory integrity but most importantly territory ownership, as well as increasing the chances of sexual competition with resident groups (see Bonadonna et al. 2014). Similar patterns of territorial responses toward unfamiliar groups—which align with the predictions of the threat level hypothesis (Temeles 1994)—are also found across taxa and signal types [e.g., green woodhoopoes *Phoeniculus purpureus* in Radford (2005); Eurasian badgers (*Meles meles*) in Palphramand and White 2007; reviewed in Christensen and Radford 2018)], though “dear-enemy” dynamics appear to be more common in solitary and pair-living territorial animals (Temeles 1994). A better understanding of rare dispersal events in indris—as well as future playback studies focusing on same-sex responses to solo songs—would help us to shed light on the ultimate mechanisms for the observed differences in aggression levels.

Finally, we tested whether acoustic information about group size may allow numerical assessment in the listener, thus playing a role in evaluating threat levels of approaching competitors. For example, playback studies in other primates have shown that territory owners can use acoustic cues to adjust their reaction to a simulated intrusion based on opponent group's size (McComb et al. 1994; Wilson et al. 2001; Kitchen 2004; Crofoot et al. 2008; Meunier et al. 2012). However, we did not detect such an effect in our study, as the number of callers in stimulus songs did not impact the magnitude of territorial responses in the test groups (Table 1). A possible explanation for this finding is that group size may not be a determinant during inter-group contests in indris, as floaters and neighbors rarely outnumber the resident family group. Moreover, only the adult pair—and more frequently the adult male—usually takes part in such territorial contests. Therefore, strong selection plausibly

does not act on the ability to perform numerical assessment of the opponents in this species. In species where the number of potential opponents is highly variable and the outcome of territorial contests strongly depends on numerical imbalance, territory holders were indeed shown to perform numerical assessment [e.g., chimpanzees *Pan troglodytes* (Wilson et al. 2001); spotted hyenas *Crocuta crocuta* (Benson-Amram et al. 2011); reviewed in Benson-Amram et al. 2018]. Additional information about the frequency of individual versus group dispersal and the associated threat levels would provide us with a better picture for generating predictions and designing further studies about territorial responses in indris based on intruders' number. Indri groups also did not reply to stimulus songs in nearly one third of trials, and none of the predictors could explain this variation. Stimulus songs may always be responded to when the threat of an intrusion is perceived, so that the response per se to a playback song may not have substantial discriminating value. Alternatively, modeling probabilities to reply to sudden close-range stimulus songs may require the inclusion of additional predictors, such as the prior history of interactions among groups, presence/absence of offspring, or knowledge about specific resource holding potentials at a given time. Indeed, increasing evidence shows that particularly among long-term neighbors, the magnitude of territorial responses also depends upon the prior history of interactions among groups and/or the caller group's dominance status (Christensen and Radford 2018), rather than on a general rule differentiating neighbors from strangers (Stoddard et al. 1990; Nowicki et al. 2002). For instance, in a study on howler monkeys *Alouatta palliata*, Hopkins (2013) showed that the likelihood of approach during naturally occurring howls depends on the dominance status of the calling group relative to that of the receiver. Furthermore, the reproductive status of an individual may influence its willingness to approach an intruder. For example, females carrying new borns may avoid stranger males while lactating (Ren et al. 2011) but approach them when fertile (Palombit, 1994; Bonadonna et al. 2014). Future studies in indris should include these additional variables as putative predictors to model territorial responses at a finer scale (Christensen and Radford 2018).

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Conflict of interest

The authors declare that they have no conflict of interest.

Authors' Contributions

G.S., V.T., G.B., C.D., and D.V. conducted data collection. G.S. and M.G. conducted the statistical analyses. G.S., M.G., V.T., and C.G. prepared the final version of the manuscript.

References

- Akçay Ç, Reed VA, Campbell SE, Templeton CN, Beecher MD, 2010. Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping. *Anim Behav* 80:1041–1047.
- Akçay Ç, Wood WE, Searcy WA, Templeton CN, Campbell SE, Beecher MD, 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Anim Behav* 78:97–102.
- Arbib MA, Liebal K, Pika S, 2008. Primate vocalization, gesture, and the evolution of human language. *Curr Anthropol* 49:1053–1076.
- Baker-Medard MSA, Baker MC, Logue DM, 2013. Chorus song of the indri (*Indri indri*: primates, Lemnidae): group differences and analysis of within-group vocal interactions. *Int J Comp Psychol* 26:241–255.
- Barr DJ, 2013. Random effects structure for testing interactions in linear mixed-effects models. *Front Psychol* 4:328.
- Barton K, 2018. *MuMIn: Multi-Model Inference*. R package version 1.42.1.
- Becker PH, 1982. The coding of species-specific characteristics in bird sounds. In: Kroodsma DE, Miller EH, editors. *Acoustic Communication in Birds*. New York (NY): Academic Press. 214–244.
- Beecher MD, Akçay Ç, Campbell SE, 2020. Birdsong learning is mutually beneficial for tutee and tutor in song sparrows. *Anim Behav* 166: 281–288.
- Beletsky LD, Orians GH, 1989. Familiar neighbors enhance breeding success in birds. *Proc Natl Acad Sci USA* 86:7933–7936.
- Belle S, Estrada A, Garber P, 2013. Spatial and diurnal distribution of loud calling in black howlers (*Alouatta pigra*). *Int J Primatol* 34:1209–1224.
- Benson-Amram S, Gilfillan G, McComb K, 2018. Numerical assessment in the wild: insights from social carnivores. *Philos Trans R Soc B* 373:20160508.
- Benson-Amram S, Heinen VK, Dryer SL, Holekamp KE, 2011. Numerical assessment and individual call discrimination by wild spotted hyenas, *Crocuta crocuta*. *Anim Behav* 82:743–752.
- Benten A, Cross HB, Tinnesand HV, Zedrosser A, Rosell F, 2020. Distant neighbours: friends or foes? Eurasian beavers show context-dependent responses to simulated intruders. *Behav Ecol Sociobiol* 74:17.
- Bergman TJ, 2010. Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proc Royal Soc B* 277:3045–3053.
- Bonadonna G, Torti V, Randrianarison RM, Martinet N, Gamba M, Giacomini C, 2014. Behavioral correlates of extra-pair copulation in Indri indri. *Primates* 55:119–123.
- Bonadonna G, Torti V, Sorrentino V, Randrianarison RM, Zaccagno M et al., 2017. Territory exclusivity and intergroup encounters in the indris (Mammalia: primates: indridae: *indri indri*) upon methodological tuning. *Eur Zool J* 84:238–251.
- Bonadonna G, Zaccagno M, Torti V, Valente D, De Gregorio C et al., 2020. Intra- and intergroup spatial dynamics of a pair-living singing primate, *Indri indri*: a multiannual study of three indri groups in Maromizaha Forest, Madagascar. *Int J Primatol* 41:224–245.
- Brooks RJ, Falls JB, 1975. Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. *Can J Zool* 53:1412–1420.

- Carlson NV, Kelly EM, Couzin I, 2020. Individual vocal recognition across taxa: a review of the literature and a look into the future. *Philos Trans R Soc B* 375:20190479.
- Cheney DL, Seyfarth RM, 1982. Recognition of individuals within and between groups of free-ranging vervet monkeys. *Integr Comp Biol* 22: 519–529.
- Cheney DL, Seyfarth RM, 2010. Primate Communication and Human Language: continuities and Discontinuities. In: Kappeler PM, Silk J, editors. *Mind the Gap: Tracing the Origins of Human Universals*. Berlin, Heidelberg, Germany: Springer. 283–298.
- Christensen C, Radford AN, 2018. Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behav Ecol* 29:1004–1013.
- Clink DJ, Hamid Ahmad A, Klinck H, 2020. Gibbons aren't singing in the rain: presence and amount of rainfall influences ape calling behavior in Sabah, Malaysia. *Sci Rep* 10:1–13.
- Cowlshaw G, 1992. Song function in gibbons. *Behaviour* 121:131–153.
- Crofoot MC, Gilby IC, Wikelski MC, Kays RW, 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proc Natl Acad Sci USA* 105:577–581.
- Dalton B, Settle R, Medley K, Mathis A, 2020. When neighbors cheat: a test of the dear enemy phenomenon in southern red-backed salamanders. *Behav Ecol Sociobiol* 74:56.
- De Gregorio C, Zanolli A, Valente D, Torti V, Bonadonna G et al., 2019. Female indris determine the rhythmic structure of the song and sustain a higher cost when the chorus size increases. *Curr Zool* 65:89–97.
- Deppe AM, Wright PC, Szelistowski WA, 2009. Object permanence in lemurs. *Anim Cogn* 12:381–388.
- Dobson AJ, 2002. *An Introduction to Generalized Linear Models*. 2nd edn. Boca Raton (FL): Chapman and Hall/CRC Press.
- Dunbar RIM, Shultz S, 2007. Evolution in the social brain. *Science* 317: 1344–1347.
- Ferrandiz-Rovira M, Zidat T, Dupont P, Berger V, Rézouki C, Cohas A, 2020. Neighborhood bully: no difference in territorial response toward neighbors or strangers in marmots. *Behav Ecol* 31:1129–1141.
- Fichtel C, Kappeler PM, 2010. Human universals and primate symplesiomorphies: establishing the lemur baseline. In: Kappeler PM, Silk J, editors. *Mind the Gap: Tracing the Origins of Human Universals*. Berlin, Heidelberg, Germany: Springer. 395–426.
- Fichtel C, Dinter K, Kappeler PM, 2020. The lemur baseline: how lemurs compare to monkeys and apes in the primate cognition test battery. *PeerJ* 8: e10025.
- Field A, 2005. *Discovering Statistics Using SPSS*. London: Sage Publications.
- Fisher J, 1954. Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. *Evolution as a Process*. London: Allen and Unwin. 71–83.
- Forstmeier W, Schielzeth H, 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav Ecol Sociobiol* 65:47–55.
- Gamba M, Torti V, Estienne V, Randrianarison RM, Valente D et al., 2016. The indris have got rhythm! Timing and pitch variation of a primate song examined between sexes and age classes. *Front Neurosci* 10:249.
- Génin F, 2021. Speciation by sensory drive in the *Paragalago zanzibaricus* species complex. *Int J Primatol* 42:478–498.
- Getty T, 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? *Integr Comp Biol* 27:327–336.
- Giacoma C, Sorrentino V, Rabarivola C, Gamba M, 2010. Sex differences in the song of *Indri indri*. *Int J Primatol* 31:539–551.
- Godard R, 1993. Tit for tat among neighboring hooded warblers. *Behav Ecol Sociobiol* 33:45–50.
- Grabowska-Zhang AM, Wilkin TA, Sheldon BC, 2012. Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behav Ecol* 23:322–333.
- Haimoff EH, 1986. Convergence in the duetting of monogamous Old World primates. *J Hum Evol* 15:51–59.
- Ham S, Hedwig D, Lappan S, Choe JC, 2016. Song functions in nonduetting gibbons: evidence from playback experiments on Javan gibbons (*Hylobates moloch*). *Int J Primatol* 37:225–240.
- Herbinger I, Papworth S, Boesch C, Zuberbühler K, 2009. Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. *Anim Behav* 78:1389–1396.
- Hervieu J, 1960. *Notice sur Les Cartes pe 'Dologiques de Reconnaissance 1/200000 Feuille n3. Brickaville- Moramanga*. Tananarive, Madagascar: IRSM. 67
- Hopkins ME, 2013. Relative dominance and resource availability mediate mantled howler (*Alouatta palliata*) spatial responses to neighbors' loud calls. *Int J Primatol* 34:1032–1054.
- Hyman J, 2002. Conditional strategies in territorial defense: do Carolina wrens play tit-for-tat? *Behav Ecol* 13:664–669.
- Hyman J, Hughes M, 2006. Territory owners discriminate between aggressive and nonaggressive neighbours. *Anim Behav* 72:209–215.
- Isler K, Christopher Kirk E, Miller JMA, Albrecht GA, Gelvin BR, Martin RD, 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J Hum Evol* 55:967–978.
- Kessler SE, Radespiel U, Hasiniaina AIF, Nash LT, Zimmermann E, 2018. Does the grey mouse lemur use agonistic vocalisations to recognise kin? *Contrib Zool* 87:261–274.
- Kitchen DM, 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Anim Behav* 67:125–139.
- Kittler K, Kappeler PM, Fichtel C, 2018. Instrumental problem-solving abilities in three lemur species (*Microcebus murinus*, *Varecia variegata*, and *Lemur catta*). *J Comp Psychol* 132:306–314.
- Kittler K, Schnoell AV, Fichtel C, 2015. Cognition in ring-tailed lemurs. *Folia Primatol* 86:106–116.
- Krams I, Krama T, Igaune K, Mänd R, 2008. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav Ecol Sociobiol* 62:599–605.
- Kroodsma DE, 1989. Suggested experimental designs for song playbacks. *Anim Behav* 37:600–609.
- Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu WC, 2001. Pseudoreplication in playback experiments, revisited a decade later. *Anim Behav* 61:1029–1033.
- Liebgold EB, Cabe PR, 2008. Familiarity with adults, but not relatedness, affects the growth of juvenile red-backed salamanders (*Plethodon cinereus*). *Behav Ecol Sociobiol* 63:277–284.
- Macedonia JM, 1993. The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatol* 61:186–217.
- Macedonia JM, 1990. What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed Lemurs. *Ethology* 86:177–190.
- Maciej P, Patzelt A, Ndao I, Hammerschmidt K, Fischer J, 2013. Social monitoring in a multilevel society: a playback study with male Guinea baboons. *Behav Ecol Sociobiol* 67:61–68.
- Maretti G, Sorrentino V, Finomana A, Gamba M, Giacoma C, 2010. Not just a pretty song: an overview of the vocal repertoire of *Indri indri*. *J Anthropol Sci* 88:151–165.
- Masters JC, Génin F, 2016. Why the strepsirhines are not primitive. In: Norscia I, Palagi E, editors. *The Missing Lemur Link. An Ancestral Step in the Evolution of Human Behaviour*. Cambridge: Cambridge University Press. xxvi–xxxi.
- McComb K, Packer C, Pusey A, 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Anim Behav* 47: 379–387.
- Meunier H, Molina-Vila P, Perry S, 2012. Participation in group defence: proximate factors affecting male behaviour in wild white-faced capuchins. *Anim Behav* 83:621–628.
- Mitani JC, 1984. The behavioural regulation of monogamy in gibbons (*Hylobates muelleri*). *Behav Ecol Sociobiol* 15:225–229.
- Mitani JC, 1985. Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets. *Int J Primatol* 6:193–200.
- Mitani JC, 1987. Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behav Ecol Sociobiol* 20:265–269.
- Nakagawa S, Johnson PCD, Schielzeth H, 2017. The coefficient of determination r and intra-class correlation coefficient from generalized linear

- mixed-effects models revisited and expanded. *J R Soc Interface* 14: 20170213.
- Nieuwenhuis R, Te Grotenhuis M, Pelzer B, 2012. influence.me: tools for detecting influential data in mixed effects models. *R J* 4:38–47.
- Norscia I, Palagi E, 2016. *The Missing Lemur Link: An Ancestral Step in the Evolution of Human Behaviour*. Cambridge: Cambridge University Press.
- Nowicki S, Searcy WA, Peters S, 2002. Quality of song learning affects female response to male bird song. *Proc Biol Sci* 269:1949–1954.
- O'Brien RM, 2007. A caution regarding rules of thumb for Variance Inflation Factors. *Qual Quant* 41:673–690.
- Oda R, 2001. Lemur vocal communication and the origin of human language. In: Matsuzawa T, editor. *Primate Origins of Human Cognition and Behavior*. Tokyo, Japan: Springer Japan. 115–134.
- Oda R, 2002. Individual distinctiveness of the contact calls of ring-tailed lemurs. *Folia Primatol* 73:132–136.
- Olendorf R, Getty T, Scribner K, Robinson SK, 2004. Male red-winged blackbirds distrust unreliable and sexually attractive neighbours. *Proc Royal Soc B* 271:1033–1038.
- Palombit RA, 1994. Extra-pair copulations in a monogamous ape. *Anim Behav* 47: 721–723.
- Palphramand KL, White PCL, 2007. Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. *Anim Behav* 74:429–436.
- Pereira ME, Macedonia JM, 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Anim Behav* 41:543–544.
- Pollock JI, 1975. Field observations on indri indri: a preliminary report. In: Tattersall I, Sussman RW, editors. *Lemur Biology*. Boston (MA): Springer US. 287–311.
- Pollock JI, 1986. The song of the Indris (Indri indri; Primates: lemuroidea): natural history, form, and function. *Int J Primatol* 7:225–264.
- Powzyk J, Thalmann U, 2004. Indri indri, Indri. In: Goodman SM, Benstead JP, editors. *The Natural History of Madagascar*. Chicago (IL): University of Chicago Press. 1342–1345.
- Radford AN, 2005. Group-specific vocal signatures and neighbour–stranger discrimination in the cooperatively breeding green woodhoopoe. *Anim Behav* 70:1227–1234.
- Raemaekers JJ, Raemaekers PM, 1985. Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. *Anim Behav* 33:481–493.
- Randrianarison RMS, Rajaonson A, Ralison JM, Rabemananjara Z, Andrianantenaina TD et al., 2015. Local socio-economic effects of protected area conservation: the case of Maromizaha forest, Madagascar. *Madag Conserv Dev* 10:93–97.
- Randrianarison RM, (2019). Eco-biologie et complexe régurgitation-reingestion de la population d'Indri indri (Gmelin, 1788), forêt pluviale de Maromizaha, est de Madagascar [PhD thesis]. [Antananarivo, Madagascar]: University of Antananarivo.
- R Core Team, (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ren B, Li D, He X, Qiu J, Li M, 2011. Female resistance to invading males increases infanticide in langurs. *PLoS ONE* 6:e18971.
- Santos LR, Mahajan N, Barnes J, 2005. How prosimian primates represent tools: experiments with two lemur species (*Eulemur fulvus* and *Lemur catta*). *J Comp Psychol* 119:394–403.
- Scheumann M, Linn S, Zimmermann E, 2017. Vocal greeting during mother-infant reunions in a nocturnal primate, the gray mouse lemur (*Microcebus murinus*). *Sci Rep* 7:10321.
- Schielzeth H, Forstmeier W, 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behav Ecol* 20:416–420.
- Sekulic R, Chivers DJ, 1986. The significance of call duration in howler monkeys. *Int J Primatol* 7:183–190.
- Seppä T, Laurila A, Peuhkuri N, Piironen J, Lower N, 2001. Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles. *Can J Fish Aquat Sci* 58:1380–1385.
- Sievers C, Gruber T, 2016. Reference in human and non-human primate communication: what does it take to refer? *Anim Cogn* 19:759–768.
- Stoddard PK, Beecher MD, Horning CL, Campbell SE, 1991. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behav Ecol Sociobiol* 29:211–215.
- Stoddard PK, Beecher MD, Horning CL, Willis MS, 1990. Strong neighbor-stranger discrimination in song sparrows. *Condor* 92:1051–1056.
- Teixidor P, Byrne RW, 1997. Can spider monkeys (*Ateles geoffroyi*) discriminate vocalizations of familiar individuals and strangers? *Folia Primatol* 68: 254–264.
- Temeles EJ, 1994. The role of neighbours in territorial systems: when are they “dear enemies”? *Anim Behav* 47:339–350.
- Thalmann U, Geissmann T, Simona A, Mutschler T, 1993. The indris of Anjanaharibe-Sud, northeastern Madagascar. *Int J Primat* 14:357–381.
- Torti V, Bonadonna G, De Gregorio C, Valente D, Randrianarison RM et al. 2017. An intra-population analysis of the indris' song dissimilarity in the light of genetic distance. *Sci Rep* 7: 10140.
- Torti V, Gamba M, Rabemananjara ZH, Giacomina C, 2013. The songs of the indris (Mammalia: primates: indridae): contextual variation in the long-distance calls of a lemur. *Ital J Zool* 80:596–607.
- Torti V, Sorrentino V, Giacomina C, Gamba M, 2010. Acoustic potential for reference-like communication in wild indris. *The Evolution of Language*. Singapore: World Scientific. 505–506.
- Torti V, Valente D, De Gregorio C, Comazzi C, Miaritsoa L et al., 2018. Call and be counted! Can we reliably estimate the number of callers in the indri's (*Indri indri*) song? *PLoS ONE* 13:e0201664.
- Waser PM, 1977. Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. *Behaviour* 60: 28–74.
- Wich SA, Assink PR, Becher F, Sterck EHM, 2002. Playbacks of loud calls to wild Thomas Langurs (Primates; Presbytis thomasi): the effect of location. *Behaviour* 139:65–78.
- Wilson ML, Hauser MD, Wrangham RW, 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim Behav* 61:1203–1216.
- Ydenberg RC, Giraldeau LA, Falls JB, 1988. Neighbours, strangers, and the asymmetric war of attrition. *Anim Behav* 36:343–347.
- Zanoli A, Gregorio CD, Valente D, Torti V, Bonadonna G et al. 2020. Sexually dimorphic phrase organization in the song of the indris (*Indri indri*). *Am J Primatol* 82:e23132.