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Intra- and Intergroup Spatial Dynamics of a Pair-Living Singing Primate, *Indri indri*: A Multiannual Study of Three Indri Groups in Maromizaha Forest, Madagascar

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Abstract

Territorial pair-living species tend to occupy and defend stable areas, assumed to contain all the resources needed for the lifetime of the group. Furthermore, groups have to mediate spatial relationships with neighboring groups. We investigated the relationship between social and spatial dynamics at the intra- and intergroup level in a pair-living territorial singing primate: the indri (*Indri indri*). We collected spatial data on three neighboring groups during 396 sampling days between 2009 and 2014 in Maromizaha forest, Madagascar. We evaluated the stability of territories in terms of size and location using minimum convex polygons, defined the presence and stability of core areas, and investigated if singing locations and intergroup encounters were concentrated in the core areas. Territories were generally stable in location and size, although some degree of territorial shift occurred, leading to readjustment of intergroup spacing. Groups had core areas that were not stable across years but were concentrated in the area of the territories that groups occupy consistently over time (stable areas). Singing locations were equally distributed inside and outside core areas, suggesting an even distribution through the territories; meanwhile 9 of 12 intergroup encounters took place in the core areas at the edge of territories. Together, our results support the pattern of territorial stability predicted for a pair-living species, where groups regulate territory exclusivity and spacing with neighbors. Singing behavior also plays an important role in mediating intergroup spatial

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dynamics. The spatial pattern we found in indris is comparable with that found in other territorial and pair-living primates with different ecological needs, suggesting that in addition to ecological factors, social dynamics influence intergroup spatial dynamics.

Introduction

Animals adjust their spatial distribution to balance competing demands such as feeding, defending resources, reproducing, dealing with the presence of neighboring individuals or groups, and avoiding predators (Beyer *et al.* 2010; Lazaro-Perea 2001; Waser and Wiley 1979). The area where animals range to meet their survival needs is referred to as a home range (Burt 1943). One way to regulate the spacing between neighboring individuals or social units is to defend the exclusive use of an area against the intrusion of conspecifics, which we define as a territory and implies limited or no overlap between areas occupied by neighboring groups (Burt 1943; Clutton-Brock 1974; Maher and Lott 1995). When groups defend and exclusively occupy their entire home range, territory and home range coincide (Burt 1943). In territorial species, animals exhibit aggression toward conspecifics attempting to enter a territory (Grant *et al.* 1992). Strategies of territorial advertisement and defense may influence space use to maintain exclusive access to resources (Brown and Orians 1970; López-Sepulcre and Kokko 2005).

The degree of overlap between territories is the result of changing space use over time and is regulated by the stable occupation of an area, visiting certain areas more or less frequently and signaling territory occupancy to conspecifics (Van Belle and Estrada 2020). The degree of overlap between territories, although generally limited, may indicate the quality of the relationship between adjacent groups, with lower overlap indicating less tolerance against intrusions of conspecifics (Wrangham *et al.* 2007). Hence, territorial control leads to spatial dynamics that have a critical role in intergroup social dynamics at the population level (Furuichi 2020), requiring a consideration of social systems in territorial species.

In several species, and across taxa as diverse as Crustacea, Insects, Annelids, Fishes, Amphibians, and Mammals, pair-living co-occurs with a territorial model where the pattern of space use reflects mate guarding strategies and reproductive success (Clutton-Brock 1989; Emlen and Oring 1977; Lang and Jaeger 2000; Mathews 2002; Park and Choe 2003; Roberts and Ormond 1992). Territorial pair-living species tend to occupy a stable defended area that is assumed to include all the resources needed for survival and reproduction in the long term (Börger *et al.* 2008). Studies suggest that a pattern of stable use of an area over time, defined as site fidelity, is due to the predictability of food resources distribution (Asensio *et al.* 2012; Ramos-Fernandez *et al.* 2013). Furthermore, the presence of neighboring exclusive territories can limit the shift of territories over time, imposing a system of site fidelity. Consequently, site fidelity has implications for territoriality, because it can ensure limited investment in interactions with neighboring conspecifics (Bartlett *et al.* 2016). Studies of nonhuman primates have shown that when the habitat is not homogeneous, or resources are not evenly distributed in space and time, knowledge of food resource availability and

distribution can make site fidelity advantageous (Janmaat *et al.* 2009; Ramos-Fernandez *et al.* 2013; Wartmann *et al.* 2014). Site fidelity appears weaker when food resources are abundant and evenly distributed, which is more common for folivorous species, such as gorillas (*Gorilla gorilla beringei*) (Watts 1998a), although gorillas tend to limit foraging costs by balancing the intensity of use of an area with the regeneration of food resources (Watts 1998b).

The stable occupation of an area does not imply an even use of the space therein. On the contrary, the intensity of use of certain areas depends on resource distribution and interactions with conspecifics or neighboring groups. Group-living primates may use some areas of their range more intensively for resting, feeding, and social behaviors (Bates 1970). Such regions are defined as core areas and are considered to have important biological functions for survival (Asensio *et al.* 2014; Burt 1943; Samuel and Green 1988). Core areas do not necessarily coincide with the geometrical center of the range; indeed, intensively used areas can be located at the periphery of a territory or home range (Asensio *et al.* 2014), and can be more or less stable over time depending on the distribution of preferred food resources and the need for territorial defense (Asensio *et al.* 2014; Vander Wal and Rodgers 2012). The concepts of core area and territory are based on different assumptions: a core area is defined in terms of intensity of use, while a territory is defined as the area exclusively occupied and defended by a group (Asensio *et al.* 2014). Core areas can be identified within territories or in nondefended home ranges; however, a core area can be considered a territory if it represents the area of the range that is exclusively occupied and defended against intrusions (Bates 1970; Wartmann *et al.* 2014).

In addition to preferring core areas, groups may also tend to avoid other areas if there is a risk of potentially dangerous intergroup encounters (Wrangham *et al.* 2007). For example, in Javan gibbons (*Hylobates moloch*), individuals—especially males—select sleeping sites away from the location of encounters (Yi *et al.* 2020), and capuchin monkeys (*Cebus capucinus*) tend to reduce the risk of encounters by avoiding shared or peripheral areas of territories or home ranges (Tórrez-Herrera *et al.* 2020). A strategy to reduce the costs associated with territorial defense is the use of signals that allow long-distance communication, reducing the occurrence of physical encounters or fights. Loud calls play an essential role in signaling territory occupancy or defense and can trigger responses affecting the spacing patterns of neighboring groups (Cowlishaw 1992; Pollock 1986). The spatial responses to neighboring loud calls can also be influenced by groups' relative dominance and resource availability, as in howler monkeys (*Alouatta palliata*) (Hopkins 2013). The pattern of emission of such signals within a territory depends on the broadcast distance, the cost of emission, and the behavioral response of the receivers (da Cunha and Byrne 2006; Van Belle *et al.* 2013). In wild gray-cheeked mangabeys (*Lophocebus albigena*), for example, long-distance calls can influence the movements of resident individuals with respect to feeding resources (Brown, special issue).

Because loud calls can travel long distances, the broadcasting location in a relatively small territory does not limit communication with neighboring groups. Groups can advertise the occupancy of a territory and regulate intergroup spacing without needing to concentrate loud calls at the boundaries. Indeed, when the function of the call is to advertise territory occupancy and defensive potential, loud calls tend to be spread out within a territory, to advertise occupation (da Cunha and Byrne 2006).

The indri (*Indri indri*) is a pair-living primate that lives in groups of two to six individuals, consisting of a reproductive pair and their offspring (Pollock 1986). Genetic monogamy is the norm in this species (Bonadonna *et al.* 2019), and only one case of extra-pair copulation has been reported between two reproductive individuals of neighboring groups (Bonadonna *et al.* 2014). Individuals pair for years. Most reproductive pairs in our study population in Maromizaha, Madagascar, have been together since they were habituated in 2009, although rare cases of takeover or new pairing following the death of the partner have been reported (Bonadonna *et al.* 2019).

Both sexes disperse in indris, and in our study population, offspring remain with the family group for 4 years, on average (*unpubl. data*). Each group's range is an exclusive and defended area; the home range coincides with the territory and there is little or no overlap between neighboring territories. The ranging pattern does not indicate a constant patrolling of the boundaries and groups take *ca.* 2 weeks to range in the whole territory, requiring at least 16 days of observation to reach an accurate estimate of territory size (Bonadonna *et al.* 2017; Pollock 1986).

Indris emit songs in which the number of singers ranges from two—usually the reproductive pair—to five (Torti *et al.* 2018). The song is a cost-efficient way to communicate over long distances and one of the main functions is to regulate territorial occupancy, in addition to broadcasting individual cues (Gamba *et al.* 2016; Torti *et al.* 2017). Advertisement and territorial songs have different characteristics and can be recognized from their acoustic structure and the context of emission. Advertisement songs are emitted in the absence of visual contact between groups, they are shorter in duration, and the overlap between notes is limited. Territorial songs are emitted only when groups are in visual contact on a territorial boundary, they can last five times longer than the average advertisement song and individuals' contributions overlap highly (Torti *et al.* 2013). Intergroup encounters are infrequent (on average one encounter every 20 days) and restricted to the peripheral areas of the territory (on average within 22 m of the boundaries). In the majority of cases (86%), the encounters are solved with the emission of territorial songs and encounters rarely (13%) involve chases and physical fights (Bonadonna *et al.* 2017).

We investigated the relationships between social and spatial dynamics in indris and tested whether differential intensity of space use within a territory is related to intergroup dynamics. Because of the fine regulation of territory exclusivity between neighboring groups and the rare use of songs among primates, the indri is an interesting model to study the implications of space use for intergroup dynamics over time. We aim to extend previous findings concerning the spatial behavior of this species (Bonadonna *et al.* 2017), investigating 1) the stability of territories across time, 2) the presence and stability of core areas over time; and 3) the spatial distribution of singing locations and intergroup encounters within the territories, comparing core areas and noncore areas.

According to the hypothesis that high territorial stability reduces the costs associated with spatial mediation between neighboring groups, indris should show a pattern of territorial stability similar to that found in other pair-living territorial primates, and that over time the pattern should reflect the history of spatial dynamics between groups (Bartlett *et al.* 2016; Fernandez-Duque 2016; Van Belle *et al.* 2018; Wartmann *et al.* 2014). Therefore, we predict that indri groups will occupy the same area across successive periods with a limited territorial shift.

Core areas are assumed to contain important resources for survival and can shift over time according to spatial needs such as the distribution of preferred food resources. However, these ecological needs might not be the only drivers of the pattern of space use and groups may also spend more time in particular areas in response to the need for exclusive territories (Asensio *et al.* 2014). We hypothesize that indri groups regulate space use according to the distribution of preferred food resources and their need for exclusive territories, resulting in changes in the intensity of space use over time. Therefore, we predict that core areas will show low stability over time.

In the indri, the overlap between territories is extremely low, and intergroup encounters have a medium risk of aggression (Koch *et al.* 2016; Wrangham 2007) and are restricted to the peripheries of territories (Bonadonna *et al.* 2017). We hypothesize that indri adopt a strategy to reduce the costs associated with territorial defense concentrating core areas in the stable and exclusive area of the territory while limiting the encounters in areas intensely used on the periphery of the territory. Hence, we predict higher intensity of use within overall stable areas—areas constantly occupied by groups across years—and a concentration of intergroup encounters in the core areas rather than in noncore areas.

Indris' calling has an effective distance that extends up to 2 km, beyond the range of a single territory (Pollock 1986; Torti *et al.* 2017), so the advertisement can reach receivers independently from the sender's location within the territory. We test the hypothesis that loud calls function to signal territory occupancy and that call distribution is spread out in the territory (da Cunha and Birne 2006). Thus, we predict that calling locations are equally distributed in the core and noncore areas.

Methods

Study Site and Subjects

The New Protected Area (*Nouvelle Aire Protégée* [NAP]) of Maromizaha (18°56′S, 48°27′E) is part of the forest corridor Ankeniheny–Zahamena (CAZ). It is located in the Alaotra–Mangoro region, in the district of Moramanga, in eastern central Madagascar. Maromizaha extends for 1880 ha covered with tropical mid-altitude (800–1200) evergreen rainforest, comprising both primary and anthropologically disturbed secondary succession, with annual rainfall of 1779 mm and an endemism of 77% (Randrianarison *et al.* 2015). This kind of forest is characterized by a single stratum 20–25 m high, above an undergrowth of plentiful shrubs and herbaceous plants (Koechlin 1972). Maromizaha includes an ecotourism area, but the indri groups included in this study are located in the off-limit research area, avoiding exposure to tourists that might affect the behavior of the focal groups.

We collected spatial data on three habituated indri groups (1MZ, 2MZ, 3MZ; Table I).

Data Collection

Researchers and trained research guides that contributed to data collection collected data on three focal groups during four study periods between 2009 and 2014 (Table I). We did not have a data set robust enough for all the three groups to analyze 2009 and

Table I Description of three study groups of indris in Maromizha forest, Madagascar, and sampling strategy

Group code	Study periods	Group size	Adult female	Adult male	Subadult female	Subadult male	Juvenile female	Juvenile male	Juvenile sex unknown	Number of locations recorded	Number of sampling days	Months sampled
1MZ	2009–2010	3	1	1	—	1	—	—	—	107	29	Dec. 2009 Apr.; Oct.–Dec. 2010
	2011	4	1	1	—	1	1	—	—	122	30	Sept.–Dec.
	2012–2013	4	1	1	1	—	1	—	—	141	45	Jan.–Feb.; Apr.–Oct.; Dec. 2012
	2014	3	1	1	—	—	1	—	—	86	32	Feb.–Apr.; June–Sept.
2MZ	2009–2010	3	1	1	—	—	—	—	1	109	33	Nov.–Dec. 2009 Mar.; Oct.–Dec. 2010
	2011	2	1	1	—	—	—	—	—	90	23	Aug.–Dec.
	2012–2013	2	1	1	—	—	1	—	—	150	45	Feb.; Apr.–Dec. 2012 Feb.–Mar. 2013
	2014	3	1	1	1	—	—	—	—	42	17	Feb.–Sept.
3MZ	2009–2010	4	1	1	—	1	1	—	—	128	40	Nov.–Dec. 2009 Feb.–Mar.; Oct.–Nov. 2010
	2011	4	1	1	—	1	1	—	—	149	38	Aug.–Dec.
	2012–2013	3	1	1	1	—	—	—	—	83	30	Apr.–July; Sept.–Dec. 2012 Feb.–Mar. 2013
	2014	4	1	1	1	—	—	1	—	84	34	Feb.–Sept.
Total										1291	396	

2013 separately (Bonadonna *et al.* 2017). Because we wanted to investigate spatial dynamics across time, we prioritized continuity and pooled data collected during November and December 2009 with data for 2010, and data collected in February and March 2013 with data for 2012.

Given the indris' diurnal habits (Pollock 1975), we started observations early in the morning, at *ca.* 06:00 h, when individuals begin to be active, and we followed groups until they became inactive at *ca.* 13:30 h. We identified individuals based on their pattern of fur color.

We recorded the location of the center of group members using a hand-held global positioning system (GPS Garmin MAP 76CSX), with an accuracy of ≤5 m. A previous study of indris' spatial behavior showed that their ranging pattern is characterized by progressive directional displacements, and a group takes *ca.* 2 weeks to visit the entire territory (Bonadonna *et al.* 2017). We followed the same methodology as in the previous study, recording a new GPS point each time the animals reached a new location after having interrupted their previous activities and had moved ≥20 m from the previous location; we defined each recorded location as a stationary area (see Lair 1987; Bonadonna *et al.* 2017). Consequently, each waypoint has a different time value, and we weighted each location based on the time indris spent in each of them. Groups visited a mean of three stationary areas per day (Table I). This method, based on biological relevance rather than arbitrary time intervals between recorded locations, allowed us to avoid autocorrelation between points while maintaining biological information. We included all waypoints recorded during focal observations in analyses.

Every time the focal group emitted a spontaneous advertisement song or was involved in intergroup encounters during focal observations, we noted the geographical coordinates. We did not use playback (which could bias singing locations).

Spatial and Statistical Analysis

We analyzed all spatial data in ArcGIS 9.3 or ArcGIS 10.1 (ESRI 2012). We calculated the linear extension of the territories using minimum convex polygon (MCP) 100% because the data set is robust enough to obtain estimates of the territories with an accuracy higher than 90% (see Bonadonna *et al.* 2017 for methodological details). We performed all statistical tests in IBM SPSS 22. We report means with their standard deviation (SD).

Territory Stability We investigated the degree of stability of territories across four study periods using three different parameters: the variability in size of a territory between two consecutive study periods, the extent of territory persistently occupied by a group across the years (overall stable area), and the difference in the geometric centroids of a territory between consecutive study periods. We report the size of territories in hectares (ha) for each study period and calculate the size variability as the absolute change in percentage of territory size between two consecutive study periods. To describe the extent of variability of territory size across years, we calculated the coefficient of variation (CV) for each group.

To obtain the persistent area occupied by a group over time, we followed the methodology described in previous studies of territories and home range stability in primates (Asensio *et al.* 2012; Bartlett *et al.* 2016; Janmaat *et al.* 2009).

We overlapped all the annual MCPs of a group first, and then calculated the Minta Index (1992):

$$\frac{\cap_{i=1}^{n} a^i}{\sqrt[n]{\Pi_{i=1}^{n} a^i}}$$

where $\cap_{i=1}^{n} a^i$ is the overall intersection of n areas (n representing the number of annual territories), and $\Pi_{i=1}^{n}$ is the product of those areas, so that $\sqrt[n]{\Pi_{i=1}^{n} a^i}$ is the geometric mean of all the territory extensions obtained for each group. The Index can range between 0% (no overlap) and 100% (complete overlap) among areas. Values between 0 and 33% are classified as low overlap, 34–66% as moderate overlap, and 67–100% as high overlap (Kernohan *et al.* 2001). We also report the percentage of overlap of annual MCP with the overall stable area for each group (and respective CV) and calculated the overlap of territories between two study periods, in terms of percentage of territories maintained in the following year.

Finally, to quantify the centroid shifts, we computed X and Y coordinates of the geometric centers of annual MCPs (100%) using the Spatial Analyst tool in ArcGis 9.3 (Hooge and Eichenlaub 1997). We then calculated the linear distance (m) between centroids observed in two consecutive periods.

Core Area Designation and Stability In our data set, the time spent by a group at each recorded GPS waypoint may vary, depending on how long a group remained stationary. Hence, the number of waypoints does not reflect the intensity of use of an area. To measure the differential intensity of use within each territory, we created a grid with hexagonal cells of 0.5 ha each, using the ArcGis extension Patch Analyst (Asensio *et al.* 2012; Rempel *et al.* 2008; Rempel and Kaufmann 2003). By summing the minutes spent at each waypoint included in a cell, considering only cell grids containing stationary area centroids, we obtained the cumulative time spent at each hexagon by a group.

To evaluate differential intensity of use throughout the territory, we used ArcGis to identify four classes of intensity of cell use based on their time value. By setting 25% thresholds in the distribution of time values, we obtained a map showing four categories of intensity of use throughout the territory, with the lowest 25% representing the least most intensely used cells and the highest 25% the most intensely used cells. We report the territory size calculated using the hexagonal grid for comparison with the MCP method in Electronic Supplementary Material (ESM) Table SI.

Next, we ordered the cells according to their time values and identified the smallest number of cells that made up to 50% of the observation time. This allowed us to identify the smallest area of the territory in which a group spent at least 50% of the time, which we defined as the core area. There was no significant correlation between the percentage of territory representing the core area and absolute territory size (Pearson's correlation: $r = 0.1$, $P = 0.656$, $N = 12$). In addition, there was no correlation between sampling effort (number of months per study period) and the size of the core area (Spearman's rho: $r_s = 0.4$, $P = 0.227$, $N = 12$).

To estimate the stability of the core areas across study periods, we quantified size variability between study periods and the Minta Index, both calculated as described for

territory stability. We defined the stable core area as the hexagons maintained consistently as core areas across study periods. We report the extent of core area shared between two consecutive periods for each group, calculated as the percentage of the core area maintained from the previous period. We obtained the proportion of core area included in the territory in two consecutive study periods by calculating the percentage of core area for one study period that was included in the MCP of the next study period. Finally, we reported the percentage of the core area included in the overall stable area of territories.

Spatial Distribution of Intergroup Encounters and Singing Locations We recorded 12 intergroup encounters during the study, 4 for each group, and noted if encounters were resolved through the emission of territorial songs or if they involved physical fights. We plotted the encounters in the territories and reported the percentage located in the core areas. To account for movements of the groups during intergroup encounters, we applied a 20 m buffer (10 m radius) to each encounter point.

We recorded 191 singing locations for the three groups during the study: 77 for 1MZ, 64 for 2MZ, and 50 for 3MZ. We plotted the singing locations on the annual core area for each of the three indri groups, then used the ArcGis tool point count to obtain the number of singing locations inside and outside the core area for each territory. We then compared the frequency of the total number of singing locations inside and outside the core areas for each group. We used a chi-squared test of goodness-of-fit ($\alpha \leq 0.05$) to compare the number of singing locations between core and noncore areas. We defined expected values based on the null hypothesis of an even spatial distribution of singing locations, given that the groups spent half of the observation time inside or outside the core areas.

Ethical Note

We conducted this study on a wild population of the Critically Endangered (IUCN 2014) species *Indri indri* in the New Protected Area (NAP) of Maromizaha (Madagascar), managed by the GERP (Group d'Étude et de Recherche sur les Primates du Madagascar). During observations, we followed the groups at 10–50 m, avoiding any unnecessary disturbance. All the groups studied have been habituated to human presence since early 2009. The groups inhabit an area of primary forest accessible only when a research permit is granted; thus none of the groups has been subjected to ecotourism. None of the field workers were in physical contact with the animals. The study followed the legal requirements of Madagascar: the Ministère de l'Environnement et des Forêts (MEF) of Madagascar reviewed and approved the research methods and issued research permits for fieldwork and data collection in Maromizaha (N° 243/09/MEF/SG/DGF/DCB.SAP/SLRSE, N° 118/10/MEF/SG/DGF/DCB.SAP/SCBSE; N° 293/10/MEF/SG/DGF/DCB.SAP/SCB, N° 274/11/MEF/SG/DGF/DCB.SAP/SCB, N°245/12/MEF/SG/DGF/DCB.SAP/SCB, N°066/14/MEF/SG/DGF/DCB.SAP/SCB; N°066/14/MEF/SG/DGF/DCB.SAP/SCB).

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Data Availability The data sets analyzed during the current study are available from the corresponding author on reasonable request.

Results

Territory Stability

The three groups tended to have stable territories across the study period (2009–2014) (Fig. 1a). The results are consistent across the three parameters considered: size variability, intragroup territory overlap, and centroid shift, although we observed a degree of flexibility in the territories (Tables II and III).

Size Variability We found an overall mean territory size of 12.7 ± SD 2.8 ha ($N = 12$), ranging 9.2–17.5 ha [with the grid method we obtained an overall mean territory size of 16.0 ± SD 2.5 ha ($N = 12$), ESM Table SI]. The overall mean difference in territory size between two consecutive study periods was 10.6 ± SD 5.5 % ($N = 9$), ranging 13–22% for group 1MZ, 4–7% for group 2MZ, and 8–12% for group 3MZ. Group 1MZ showed
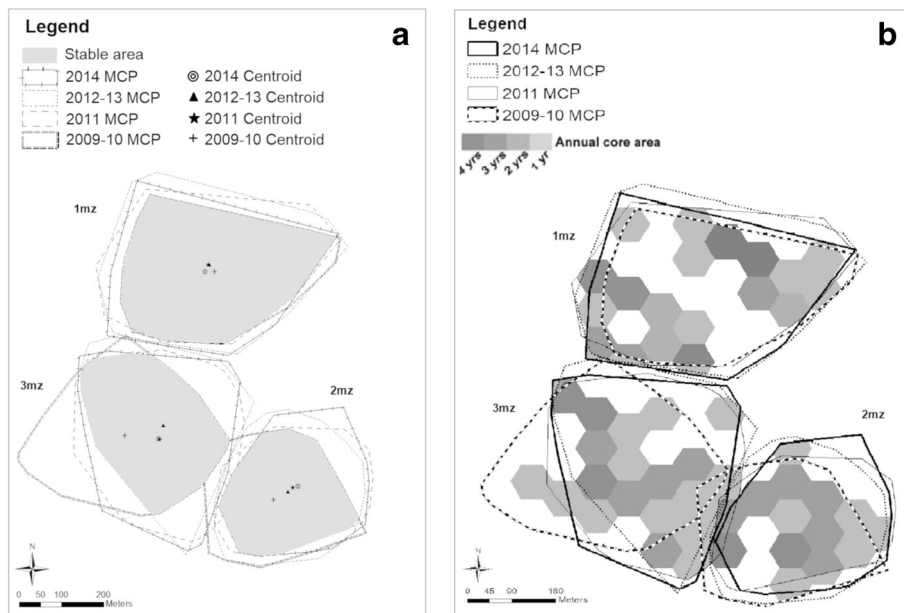

Fig. 1 Territory and core area stability for indri groups 1MZ, 2MZ, and 3MZ over four study periods (2009–2014) in Maromizaha forest, Madagascar. Dashed lines indicate the annual MCP for each group. **(a)** Intragroup territories overlap and centroids for each study period. The gray area represents the overall stable area for each group. **(b)** Overlap of core areas in each study period. Progressively darker shades represent core area shared in multiple study periods (one to four). White areas were never classified as core area during the study.

Table II Territory, core area size and stable area size for three indri groups over four study periods (2009–2014) in Maromizaha forest, Madagascar

Study period	Territory size (ha)			CA size (ha)		
	1MZ	2MZ	3MZ	1MZ	2MZ	3MZ
2009–2010	12.7	9.2	13.4	3.4	2.5	4
2011	15.3	9.6	14.7	3.8	2.2	4.2
2012–2013	17.5	10.2	12.9	4.8	3.5	3.8
2014	15	9.6	13.9	2.7	3.1	2.9
Mean ± SD	15.1 ± 2.0	9.7 ± 0.4	13.7 ± 0.9	3.6 ± 0.9	2.8 ± 0.6	3.7 ± 0.5
CV (%)	13	4.3	6.8	24	21	14.7
Overall stable area (ha)	12.2	6.88	8.7	0.9	0	0

The overall stable area is the area constantly occupied by a group across sampling periods.

the greatest increase in territory size over time, group 2MZ had the smallest and most stable territory size across years, and group 3MZ was intermediate in terms of territory size (Table II). The CVs show comparable variability in territory size across years among groups (Table II).

Intragroup Territory Overlap Groups 1MZ and 2MZ show high territorial overlap across time, and group 3MZ is at the upper limit of medium overlap (Table III). The overall mean overlap between the MCP of a given study period and the overall stable area was $63.9 \pm$ SD 14.0% ($N = 12$), ranging between 59.2% (group 3MZ) and 96.3% (group 1MZ). Although group 1MZ presents the highest value of overall overlap of its territory across time, it is also the group with the highest CV (Table II), indicating
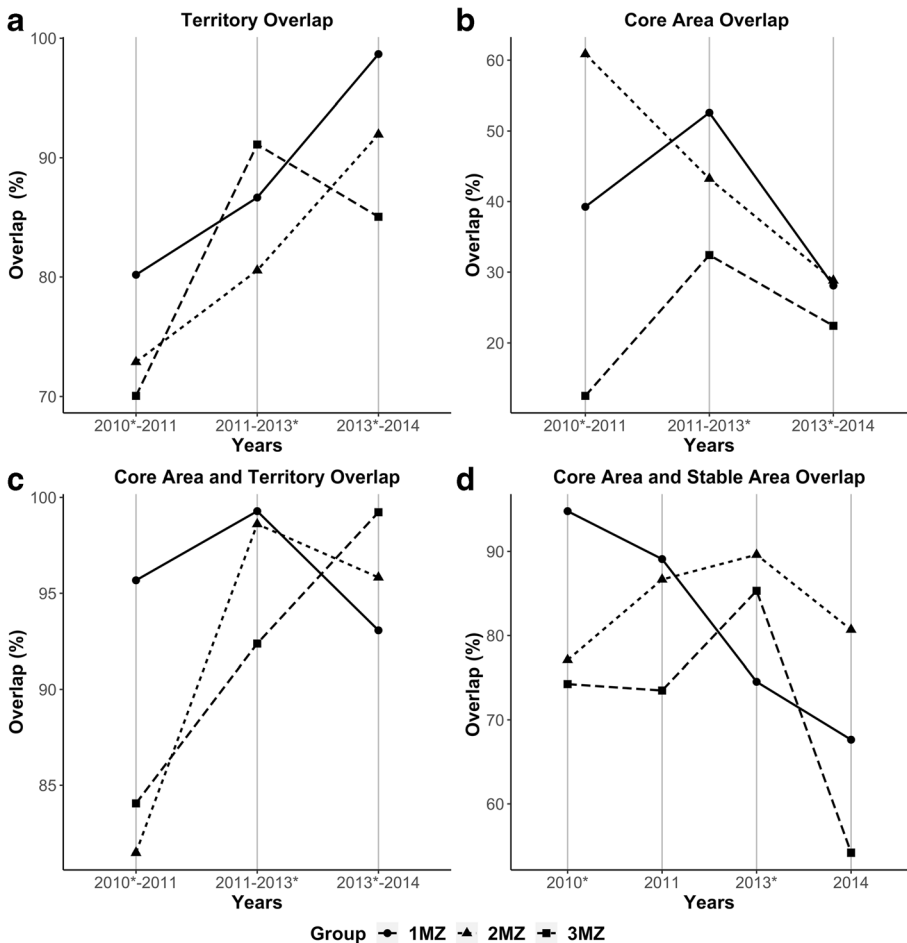
Table III Territory and core area overlap for three indri groups over four study periods (2009–2014) in Maromizaha forest, Madagascar

Group	Overlap between MCP and the overall stable area (%)			Overlap between the core area and the overall stable core area (%)		
	1MZ	2MZ	3MZ	1MZ	2MZ	3MZ
2009-2010	96.3	73.7	65.2	29.1	0	0
2011	79.6	71.1	59.2	26.2	0	0
2012-2013	69.9	66.7	67.4	20.6	0	0
2014	81.2	70.9	62.7	37.1	0	0
Mean ± SD	81.7 ±11.0	70.6 ±2.9	63.6 ±3.5	28.2 ±6.7	0	0
CV (%)	13.4	4.1	5.5	24	0	0
Minta Index (%)	81.2	70.5	63.5	27.6	0	0

Percentage of overlap between the Minimum Convex Polygon (MCP) of a sampling period and overall stable territory; percentage of overlap between the core area of a study period and the overall stable core area. We reported mean, standard deviation (SD), and coefficient of variation (CV) for each indri group. Minta Indices represent the degree of overlap for each group (high 67-100%, moderate 34-66%, low 0-33%, Kernohan *et al.* 2001).

higher flexibility in annual territory overlap with the overall stable area. The degree of territory overlap between consecutive study periods increased over time for groups 1MZ and 2MZ, but not for group 3MZ (Fig. 2a).

Centroid Shift The centroids showed little shift over time with an overall mean of 32 m ± SD 24 (N = 12), ranging between 2 m (group 1MZ) and 82 m (group 3MZ). The mean centroid shift between two consecutive periods was 14 ± SD 11 m (range: 2–22 m) for group 1MZ, 32 ± SD 19 m (range: 15–53 m) for group 2MZ, and 50 ± SD 28 m (range: 34–82 m) for group 3MZ (N = 3 for each group). We found the greatest centroid shift for group 3MZ between 2010 and 2011, which reflects the lowest values of

Fig. 2 Territory and core area overlap for indri groups over four study periods (2009–2014) in Maromizaha forest, Madagascar. Lines indicate the inter-annual variation for each group. The * indicates a study period comprising two different years (e.g., 2010* comprises 2009 and 2010). (a) Intragroup territory overlap between study periods. (b) Intragroup core area overlap between study periods. (c) Extent of core area included in the territory of the consecutive study period. (d) Extent of core area included in the overall stable area. In a, b, and c overlaps are expressed as percentages of the territory size of the consecutive study period. In d overlap is expressed as a percentage of the core area and stable area of the same study period.

interannual territory overlap found for this group (Fig. 2a). During the same time interval, we observed a 53 m centroid shift, the second largest, for the adjacent territory occupied by group 2MZ (Fig. 1a).

Intensity of Use and Core Area

We found that areas with a higher intensity of use are scattered through a group's range and can be located in the center as well as in the peripheral areas of a territory (Fig. 3). The same is true for the areas used less intensely by a group in a given study period (Fig. 3).
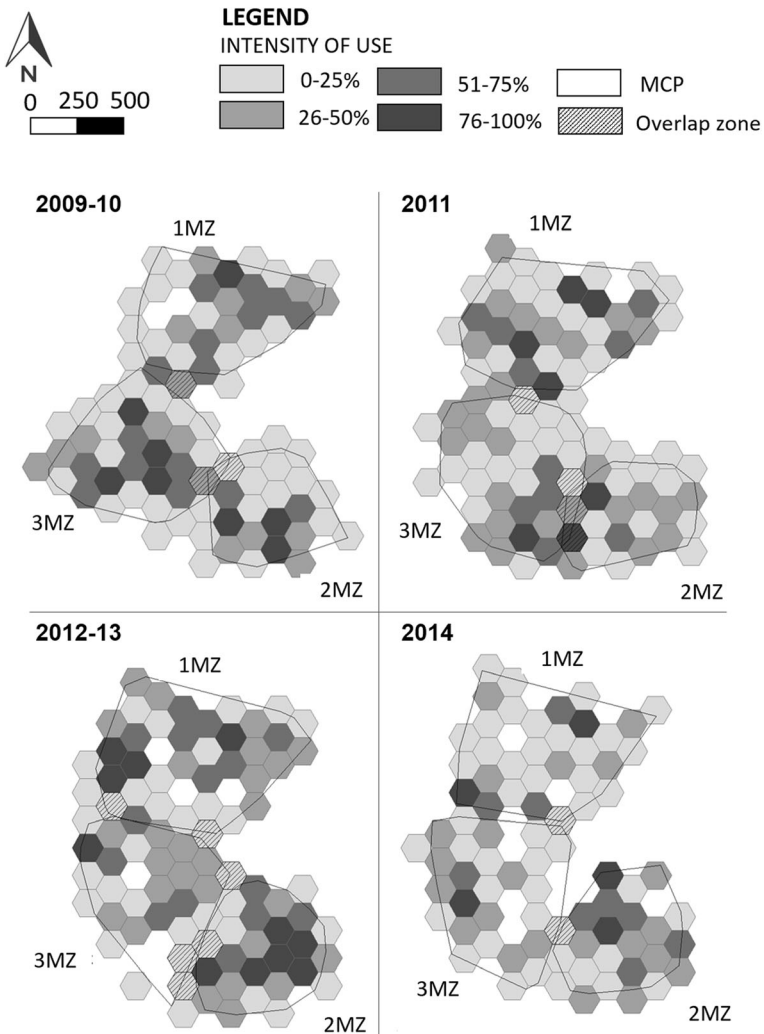
Fig. 3 Intensity of use in the territories of three neighboring groups of indris in Maromizaha forest, Madagascar, in four study periods between 2009 and 2014. Outlines represent minimum convex polygons (MCPs).

Groups spent 50% of their time in a mean area of $3.4 \pm$ SD 0.8 ha ($N = 12$), with the core area representing $26.7 \pm$ SD 4.7% ($N = 12$) of the territories (ESM Table SII). Considering each group separately across the four study periods, the core area represented $24.0 \pm$ SD 4.4% ($N = 4$) of the territory for group 1MZ, $29.0 \pm$ SD 5.1% ($N = 4$) for group 2MZ, and $27.1 \pm$ SD 4.1% ($N = 4$) for group 3MZ. Core areas of neighboring groups never overlapped during a study period but could be adjacent to each other (Fig. 4).

We found considerable variation in core area size and location across time (Table II). We found a greater change of core area size between study periods than for territory size, with an overall mean change of $22.2 \pm$ SD 18.7% in size between consecutive
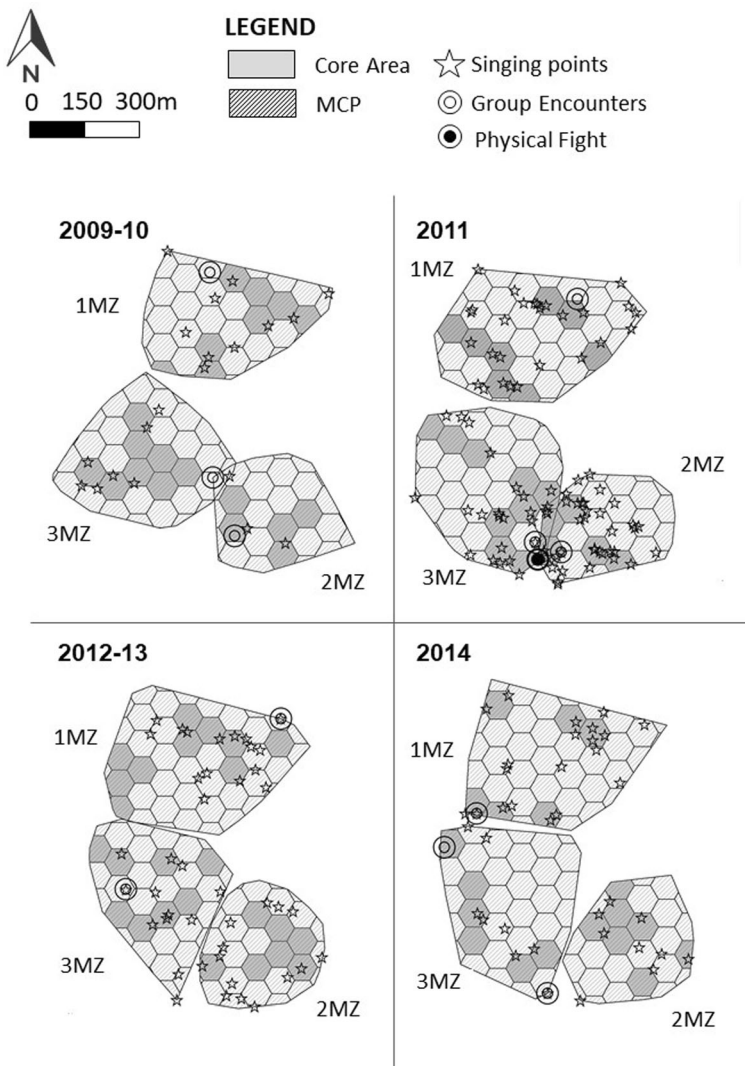

Fig. 4 Core area, spatial distribution of singing locations, and intergroup encounters in three neighboring groups indri in Maromizaha forest, Madagascar, during four study periods between 2009 and 2014.

study periods ($N = 9$). The high CVs indicate that the core area size of a group can greatly vary from one study period to another (Table II).

All three indri groups exhibited low overlap of core areas across years (Table III). Only group 1MZ showed core area overlap throughout the four study periods. Neither group 2MZ nor group 3MZ had an overall stable core area, although they occupied smaller territories than group 1MZ (Tables II and III). We found a degree of intersection in the overlap of core areas between two consecutive study periods for all groups (ESM Fig. S1). Group 2MZ showed the highest percentage of core area overlap between two consecutive periods (61%), although the overlap decreased over time. Groups 1MZ and 3MZ showed a similar change in overlap size between 2 years over time, with group 3MZ presenting the lowest values, ranging 13–32% (Fig. 2b). Overall, $93.3 \pm SD\ 6.5\%$ ($N = 9$) of core areas were still included as part of the territory in the following year. Group 1MZ showed an overlap higher than 90% in all years; the other two groups showed a general increasing trend, with the last period showing overlap values >95% (Fig. 2c). Across the study period, $78.9 \pm SD\ 11.2\ \%$ ($N = 12$) of core areas were located in the overall stable area, ranging between 54.2% (group 3MZ) and 95.8% (group 1MZ) (Fig. 2d).

Spatial Distribution of Intergroup Encounters and Singing Locations

Nine of 12 intergroup encounters were located in the core areas. All but one of the encounters were resolved through the emission of territorial songs. Groups 2MZ and 3MZ had a physical fight in 2011. Three of the four encounters recorded in 2011 involved the groups 2MZ and 3MZ, following a shift of the group 3MZ's territory toward the east that resulted in an overlap between the two groups (Fig. 4). In the following study periods, the vocal activity and intergroup encounters decreased compared to 2011, and the territories of the group 2MZ and 3MZ did not overlap (Fig. 4). Group 3MZ was larger than the other group: in 2011 group 3MZ was composed of four individuals including three singers and a 2-year-old nonsinging juvenile, meanwhile group 2MZ was composed of the reproductive pair only, after losing their infant in 2010 (Table I).

Of the 191 singing locations recorded, 98 were inside the core areas (Fig. 4). A mean of $55.9 \pm SD\ 5.2\%$ ($N = 3$ groups) of songs were emitted from the core areas. We did not find a significant difference in the frequency of singing locations in core and noncore areas for any of the three groups: for group 1MZ, 37 locations (48%) were in the core area ($\chi^2 = 0.117$, df = 1, $P = 0.732$, $N = 77$); for group 2MZ, 32 locations (50%) were in the core area ($\chi^2 = 0.000$, df = 1, $P = 1$, $N = 64$); and for group 3MZ 29 locations (58%) were in the core area ($\chi^2 = 1.280$, df = 1, $P = 0.258$, $N = 50$).

Discussion

We found that indri territories were stable in terms of both size and location over four study periods. Core areas shifted over time but remained part of the territory in successive years and tended to be concentrated in the stable area of a territory. In particular, we found indris used some core areas over several years, while other areas were never included in a core area during the study. None of the three indri groups

called more frequently from core areas than the rest of the territory, and intergroup encounters—although rare—were more frequent in peripheral core areas

Territory Stability

The indri groups showed a degree of site fidelity comparable with that of other pair-living primates: white-handed gibbons (*Hylobates lar*: Bartlett *et al.* 2016), Kloss' gibbons (*Hylobates klossii*: Tenaza 1975), titi monkeys (*Callicebus* spp.: Robinson *et al.* 1987), fat-tailed dwarf lemurs (*Cheirogaleus medius*: Fietz and Dausmann 2003), and owl monkeys (*Aotus azarae*: Wartmann *et al.* 2014). This pattern of high stability implies that a territory contains all the resources needed to support a group over the long term (Bartlett 2015; Vander Wal and Rodgers 2012). In a mainly folivorous species that occupies small territories, such as the indri, the pattern of food distribution and its availability in space and time does not seem to represent the principal variable in determining the pattern of space use.

Our results suggest that the high stability is a strategy to limit the costs of spatial competition between groups, keep exclusive use of the territory, and ensure exclusive access to the partner in a pair-living system. Once territorial boundaries are set, opportunities to shift territories without risking conflicts with neighboring groups are rare. The territorial dynamics and sequential shift observed between groups 2MZ and 3MZ (including the only case of physical fight reported in our study) suggest that territorial advertisement and defense are related to the territory exclusivity, which is considered a prerequisite in maintaining a monogamous mating system (Reichard and Boesch 2003). The group with weaker stability (3MZ) was involved in the extra-pair copulation reported in 2011 (Bonadonna *et al.* 2014), suggesting that territorial stability may coincide with social and reproductive intergroup dynamics.

Core Area

We found evidence that all the groups invested half of their time spent in stationary activities in less than a third of their territory. The intensive use of a core area within a territory is a common pattern among primates, e.g., chimpanzee (*Pan troglodytes*: Herbinger *et al.* 2001), howler monkeys (*Alouatta guariba clamitans*, *Alouatta caraya*: Agostini *et al.* 2010), owl monkeys (*Aotus azarae*: Wartmann *et al.* 2014), and gibbons (*Hylobates lar*: Asensio *et al.* 2014).

We found that core areas shift but tend to be included in the next year's territory, and they cover the whole territory over the years. Similar results have been found in multiannual studies of white-handed gibbons (Bartlett *et al.* 2016) and spider monkeys (*Ateles geoffroyi*: Asensio 2011), suggesting that a territory needs to include future core areas. Unlike the indri, white-handed gibbons and spider monkeys are highly frugivorous, and the shift of core areas has been explained by changes in the availability preferred food over time (Asensio *et al.* 2014). In contrast, a long-term study of a different population of spider monkeys found that core areas were more stable than the home range, probably owing to high fidelity to high-quality habitat (Ramos-Fernandez *et al.* 2013). This suggests that intraspecific variation can be due to the spatial

distribution of food resources (Ramos-Fernandez *et al.* 2013). Finding a similar pattern of spatial stability among species with different diets, and a different pattern between populations of the same species, suggests that resource location is important in defining space use dynamics over time, but the role of territorial defense and control of mate access in pair-living species is also a contributing factor, as mate location is less predictable than the location of food resources.

Factors such as the regeneration of young leaves (>70% of the diet, Powzyk and Mowry 2003), the distribution of preferred resources in space and time, and geographic features of territories (i.e., presence of rivers and waterfalls, topography) may also influence the differential intensity of space use in indris. Our current data do not allow us to test this hypothesis.

Group Dynamics and Intergroup Encounters

Although limited in size and occurrence compared to home range overlap in nonterritorial species, overlapping zones between territories tend to be under-used, especially when encounters with neighboring groups involve the risk of dangerous fights (Tórrez-Herrera *et al.* 2020; Wrangham *et al.* 2007). In agreement with previous findings, we found that indri territories barely overlap (Bonadonna *et al.* 2017); thus, it is not surprising that intergroup encounters are rare in this species, although they can occur. Most of the encounters were located in heavily used areas located at the periphery of territories, which suggests that spending time at the territorial border increases the probability of an intergroup encounter, despite the limited or no overlap between territories. Groups may also spend more time in areas where an intergroup encounter took place to defend a disputed area of territory. Furthermore, we found that even if core areas were located in the peripheral area of a territory, they were concentrated in the overall stable area of a territory, suggesting that indri groups concentrate their activities in areas less affected by territorial changes, which can limit the risk of encounters in contentious areas.

Through the emission of songs, indris maintain an exclusive use of the territory, limiting the necessity of physical confrontation. This strategy of territorial defense and exclusivity can also reinforce an active mate guarding strategy: having exclusive territories and minimizing the risk of physical encounters can be a strategy to monopolize access to females (Reichard and Boesch 2003). During intergroup encounters, males of territorial species can discourage neighboring males attempting to mate with the resident female (Koch *et al.* 2016), while at the same time displaying their ability to defend a territory (Kempenaers and Dhondt 1993).

A good example of the role of territorial defense on maintaining exclusive access to the partner is given by comparing intergroup encounters and extra-pair copulations rates between indris and gibbons. Intergroup encounters in indris are rare. Only one observation of extra-pair copulation has been reported (Bonadonna *et al.* 2014) and genetic monogamy seems to be the norm in this species (Bonadonna *et al.* 2019). In contrast, gibbons have a high rate of intergroup encounters, and pair-living females show higher rates of extrapair copulation compared to the indris (Barelli *et al.* 2013; Reichard and Barelli 2008).

Singing Locations

We found that the indri's advertisement songs are equally distributed inside and outside the core areas, relative to the time a group spent in those areas. The fact that core areas shift over time may explain the strategy of advertising group presence throughout their territories rather than concentrating the advertisement in areas more intensely used in the relatively short term. Indri groups emit on average 2.2 advertisement songs per day (Torti *et al.* 2013) and the signal can reach far beyond the territory, eliminating the need to broadcast the signal from certain locations so that it would reach receivers located outside the territory.

Our results are in line with the proposed role of advertisement songs for indris: maintaining territory occupancy and reducing the need to engage in costly intergroup confrontations (Geismann and Mutcschler 2006; Pollock 1986). This description fits with the model of regular advertisement of occupation, which predicts that loud calls are spread all over the range when they function to announce territory occupancy (da Cunhna and Byrne 2006). The same model has been suggested for howler monkeys (*Alouatta pigra*: Van Belle *et al.* 2013), while in Kloss's gibbons most post-dawn singing locations are in what the authors call the "most used area" (Whitten 1982). In contrast, in indris the spatial distribution of territorial songs is limited to the boundaries, fitting with a model of territorial boundary marking and defense (da Cunhna and Byrne 2006) and in accordance with the exclusive emission of territorial song in the context of intergroup encounters (Torti *et al.* 2013). In conclusion, we consider that given the pronounced territoriality of the indri, and the efficient spacing between neighboring groups, the pattern of space use in indris is influenced by intergroup dynamics and vocal communication.

The maintenance of stable and exclusive territories, as we found for indri, is a prerequisite for the evolution and maintenance of a pair-living social system and sexually or genetic monogamous mating system (Reichard 2003). However, not all pair-living primates are territorial and vice versa. A system in which pair-living and territoriality are linked may require the evolution of strategies to regulate communication and relationships between units, because units compete and are not independent of each other (Bartlett 2003; Fuentes 2000; Furuichi 2020; Tsai 2002).

From their studies on white handed gibbons, Bartlett et al. (2016) suggested that social factors can also drive space use, in addition to ecological factors, and that to better understand the behavioral ecology of a species, social units should not be considered as independent but as part of a network. We found a similar pattern in the indri, a species with a different feeding ecology from that of gibbons, but with many similarities in their social organization and vocal communication. Both social organization and ecological needs play a role in intergroup spatial and territorial dynamics, the link between social organization and external and ecological factors was suggested decades ago (Bartlett 2003; Emlen and Oring 1977; Tsai 2002). Studies of the role of ecological variables, such as the spatial and temporal distribution of preferred food resources, are needed to better understand the role of ecological factors alongside social factors, and reach a more complete understanding of the drivers behind the intergroup dynamics in a pair-living territorial singing primate.

Supporting Information

Estimates of territory size obtained with the method of the grids and minimum convex polygons (ESM Table SI), the complete data set used to conduct the analysis on the core extensions and stability (ESM Table SII), and the map showing core areas overlap between two following sampling periods for each group (ESM Fig. S1) are available online.

Author Contributions   GB, MZ, and VT developed methodology and performed the analyses. GB, MZ, VT, DV, CDG, and RMR conducted the fieldwork. CT, MG, and CG contributed in developing the methods, interpreting of the results, and provided editorial advice. GB, MZ, VT, DV, CDG, and MG wrote the manuscript.

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