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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Corresponding Author:	Giovanna Bonadonna Universita degli Studi di Torino Dipartimento di Scienze della Vita e Biologia dei Sistemi ITALY
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universita degli Studi di Torino Dipartimento di Scienze della Vita e Biologia dei Sistemi
Corresponding Author's Secondary Institution:	
First Author:	Giovanna Bonadonna
First Author Secondary Information:	
Order of Authors:	Giovanna Bonadonna
	Michele Zaccagno
	Valeria Torti
	Daria Valente
	Chiara De Gregorio
	Rose Marie Randrianarison
	Chia Tan
	Marco Gamba
	Cristina Giacoma
Order of Authors Secondary Information:	
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Abstract:	Territorial pair-living species tend to occupy stable, defended areas, assumed to contain the totality of resources needed for the lifetime of the social unit. Furthermore, groups have to mediate spatial relationships with neighboring groups. Through the analysis of territorial stability, core areas, and territorial advertisement and defense across time, the goal of this study is to investigate the relationship between social and spatial dynamics at the intra and intergroup level in a pair-living territorial singing

	primate: the indri (Indri indri) . In this study we collected spatial data on three neighboring groups during 396 sampling days between 2009 and 2014 in the 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 resulted to be stable in location and size, although we found that limited territorial shift can occur and lead to intergroup spacing readjustment. Groups have core areas with low stability across years and are concentrated in the area of the territories consistently occupied by groups over time (stable areas). Singing locations were equally distributed within and outside core areas, suggesting an even distribution through the territories; meanwhile 60% of twelve intergroup encounters took place in the core areas and were located at the periphery of territories. Together, our results confirm the pattern of territorial stability expected in a pair-living species, where individuals regulate territory exclusivity and spacing between neighboring groups. The singing behavior also plays an important role in mediating intergroup spatial dynamics. The spatial pattern we found in indris is comparable with the one found in other territorial and pair-livings primates, but with different ecological needs, suggesting that social dynamics can influence intergroup spatial dynamics.
Suggested Reviewers:	Lydia Light llight1@uncc.edu Expert in behavioral ecology and spatial dynamics of territorial monogamous primates
	Thad Bartlett thad.bartlett@utsa.edu Expert of gibbons behavioral ecology, including long term territory stability.
	Adriano Lameira arel@st-andrews.ac.uk Expert in animal vocal communication

Line 71 - replace comma with semicolon, place comma after "indeed," and chance to "intensively"
Changed, thank you.

Line 75 - add "a" before "core area" and "territory"
Added, thank you

Line 90 - change to read "groups’"
We changed groups with groups’

Line 103 - change comma to semicolon and pluralize "coincide"
Noted, thank you.

Line 105 - reword "going" to "ranging"
Changed, thank you.

Line 107-109 - wording is hard to follow - are advertisement songs different from territorial songs? Advertisement songs are produced in the absence of conspecifics whereas territorial songs are only produced during territorial disputes?
Correct, advertisement songs have different temporal and spectral features and are emitted in a different context respect to territorial songs. We better described the characteristics of the two songs and rephrased the paragraph.

Line 122 - change to read "with a tendency to maintain high territorial stability to reduce the costs"
Corrected, thank you.

Line 124-126 - It is unclear what the author is arguing here as the second half of the sentence is redundant: "higher intra-group territory overlap over time" is the same as "occupy the same area across successive periods with a limited territorial shift."
We deleted the second half of the sentence.

Line 127 - add "the" before "case" and change "folivores species" to either "folivores" or "folivorous species"
Changed, thank you.

Line 129-133 - explain how intensity of use relates to territorial defense, especially for animals who may not be using certain areas as intensively (as I imply indris would be doing) - I am not following the link because my assumption would be that the wider availability of food resources would allow indris to range based on other factors (such as social interactions - or avoidance of them) and may in fact create larger but much more stable core areas. As neighbors would presumably remain in close proximity across years but indris would be released from the pressures of patchy food resource distribution, would the defendability of a range benefit from frequent monitoring of the territorial borders? And would that not also increase the core area to most of the entire home range?

As we understand, the main question is: if groups don’t have the spatial constrain of food resources availability, why don’t expect that they would spend more time on the boundary to maximize territorial defense? To consider this hypothesis, we need to elaborate on i) why we do not expect a more intense use of the boundary in indri and ii) why a spread availability of food resources can still influence the ranging pattern in territories that include all the resources in the long term.

A previous study shows that the indri does not have a patrolling ranging pattern (Bonadonna et al. 2017) and in preliminary analyses we didn't find a concentration of core areas on the boundary of territories.
The fact that indris signal territory occupancy to conspecifics through the emission of songs can explain the efficient control of territory exclusivity without the necessity of boundary patrolling. In fact, border patrolling is not a costly efficient strategy considering the body size of the indri and its vertical climbing and leaping locomotion.
Probably, a constant territorial boundary patrol would also result in a higher inter group encounters rate, which instead is extremely low in this species. However, groups still need to maintain a control on territories' exclusivity and may spend more time in areas that can be at higher risk of conspecific intrusion or because of the history between neighboring groups (i.e. loss of territory, recent intergroup encounters, tentative of intrusion, detection of a dispersing individual in the area, …). Therefore, instead of referring to territorial defense, we now refer to territorial dynamics, a more inclusive term.
Leaves are a food resource that is available all the time but based on what has been found in other folivorous species, a differential exploitation in space and time might be required to ensure availability of preferred food resources in the long term. Because we don't have ecological data to support this hypothesis, we cannot exclude a priori an influence of ecological factors on the pattern of intensity of use of certain areas within territories.
Finally, if the core area as we defined it would occupy the entire territory, a core area wouldn't exist.

For all these reasons, we do not expect to find core areas more concentrated on territories' periphery, as it would be in case groups would stay more often on the border of their territories, and we do not exclude that ecological factors may play a role in the pattern of intensity of use. This is the reason why we do not expect to find high stability in the core area but rather a shift within the territory in response to intergroup and territorial dynamics without excluding an influence given by ecological needs.

We included information on the ranging behavior on the introduction and rephrased the paragraph in question to highlight the assumptions behind our expectation.

Line 159 - add space after parenthesis
Corrected, thank you.

Table 1 - This seems like quite a low number of locations recorded per day with sometimes less than an average of three locations sampled per day.
Yes, indeed. Sometimes a group remains in the very same location during the entire day of observation (which means one location recorded in the entire day), other times they visit 8 different locations – although very rarely -. It is not a bias or a mistake in the dataset, groups can be "stationary", and they actually do not tend to displace many times during the daily activity

period. This is also the reason why we were concerned with autocorrelation and we decided to opt for a different methodology. We made it more explicit at L200-212.

Line 166 - add "of" after "loss"
Added, thank you

Line 172-182 - I understand the desire to avoid autocorrelation but the method chosen seems too open for observer bias. The authors state that spatial data were collected ad libitum. This might be fine for projects focused on social behavior or diet, but for a project focused on ranging patterns, a more systematic approach to spatial data collection is needed. The authors describe their use of "stationary areas" but this may grossly underestimate the importance of boundary patrols or other highly relevant ranging behaviors that do not require a long period of time in one location. How far do indris travel in a day? With a seven hour activity period, it seems counterintuitive to avoid any sort of timed interval data collection (maybe to be used in conjunction with the ad libitum recording).

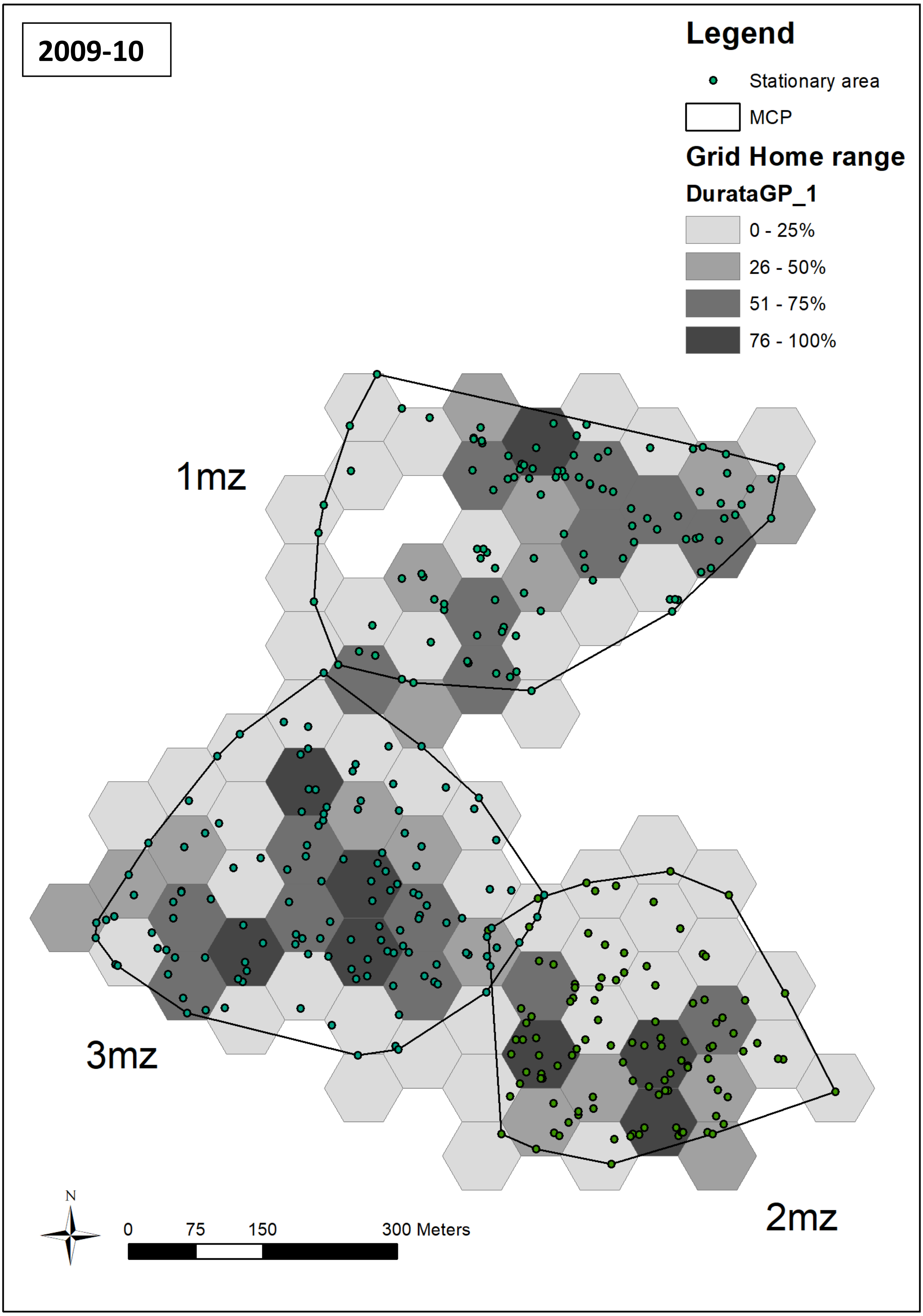
After reading Reviewer's comments we understood that our methodology sections could have been improved to present the data collection protocol in a more precise way. We mislead the use of the term "ad libitum", so we rephrased and in L200-212. – we provide the following information:

"We recorded the location of the center of the group members by using a hand-held global positioning system (GPS Garmin MAP 76CSX), with an accuracy of at least five meters. A previous study on indris' spatial behaviour (Bonadonna et al. 2017), showed that their ranging pattern is characterized by progressive directional displacements, and a group needs about 2 weeks to patrol the entire territory by visiting a minimal part of this each day. We consistently followed the methodology shown in that previous study, by recording a new GPS point each time the animals reached a new location after having interrupted their previous activities, and had moved at minimum 20 m from the previous location (see 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. On average, groups visited three stationary areas per day of observation (Table 1). This protocol, based on biological relevance rather than arbitrary time intervals between recorded locations, allowed us to avoid autocorrelation between points still maintaining biological information. We included in the analyses all waypoints recorded during the days of focal observations."

The Authors started observations early in the morning, at about 06:00, when individuals begin to be active after waking up at their sleeping trees, and followed groups until they became inactive at about 13:30. From the first sighting of the group members, to the end of the working day, the Authors recorded a new waypoint each time the animals reached a new location after having interrupted their previous activities, and had moved at minimum 20 m from the previous location (following Bonadonna et al. 2017). Every location visited by the animals during the daily ranging was therefore registered, entering a new waypoint. All the waypoints collected were used in the analysis presented in this MS.

The normal indri ranging behavior (Bonadonna et al. 2017) is characterized by movements between successive locations, that we called stationary areas, in which the animals may feed and rest, for few minutes to hours. Mean daily path length in the Maromizaha groups (1MZ, 2MZ, 3MZ) is 234.31+28.98 meters (range: 52.89 – 451.37 meters; Torti PhD Thesis, unpublished data). The Authors, by registering each visited location, did not underestimate the importance of boundary patrols or other highly relevant ranging behaviors that do not require a long period of time in one location, because they also collected locations in which the animals only passed, without resting (we labelled those waypoints “displacement locations”). We did not enter in the details of these differences because we are not presenting ranging behavior analyses here, and because we are using ALL waypoints for delineating areas at high and low intensity of use.

In the following four figures, we included maps (one for each sampling period) representing the MCPs and both the stationary areas (waypoints) and the grid cells, the latter showing also the intensity of use.
Summing the minutes spent at each waypoint included in a cell, we obtained the cumulative time spent at each hexagon by a group. We then identified core areas as the smallest area of the territory in which a group spent at least 50% of its time.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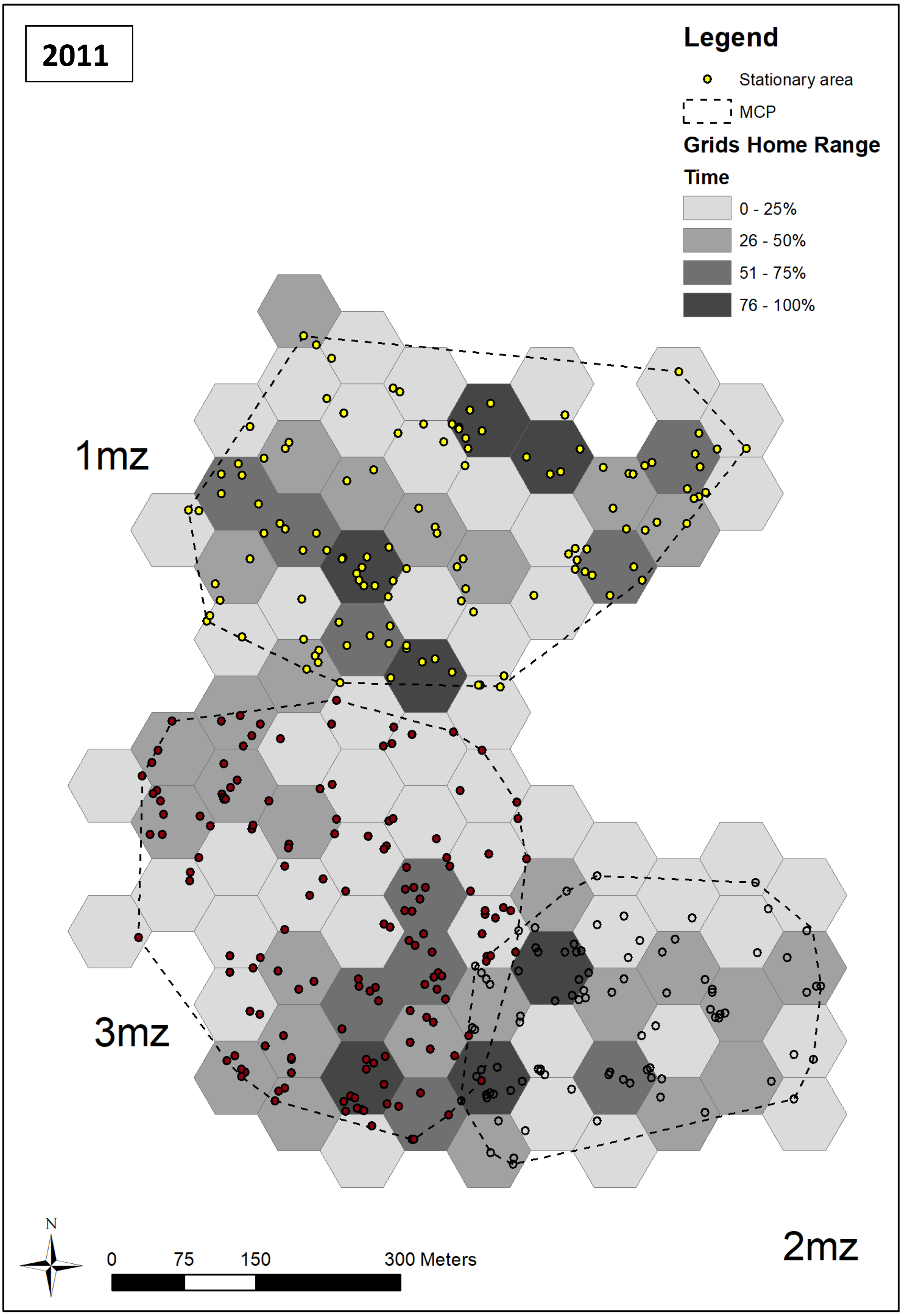
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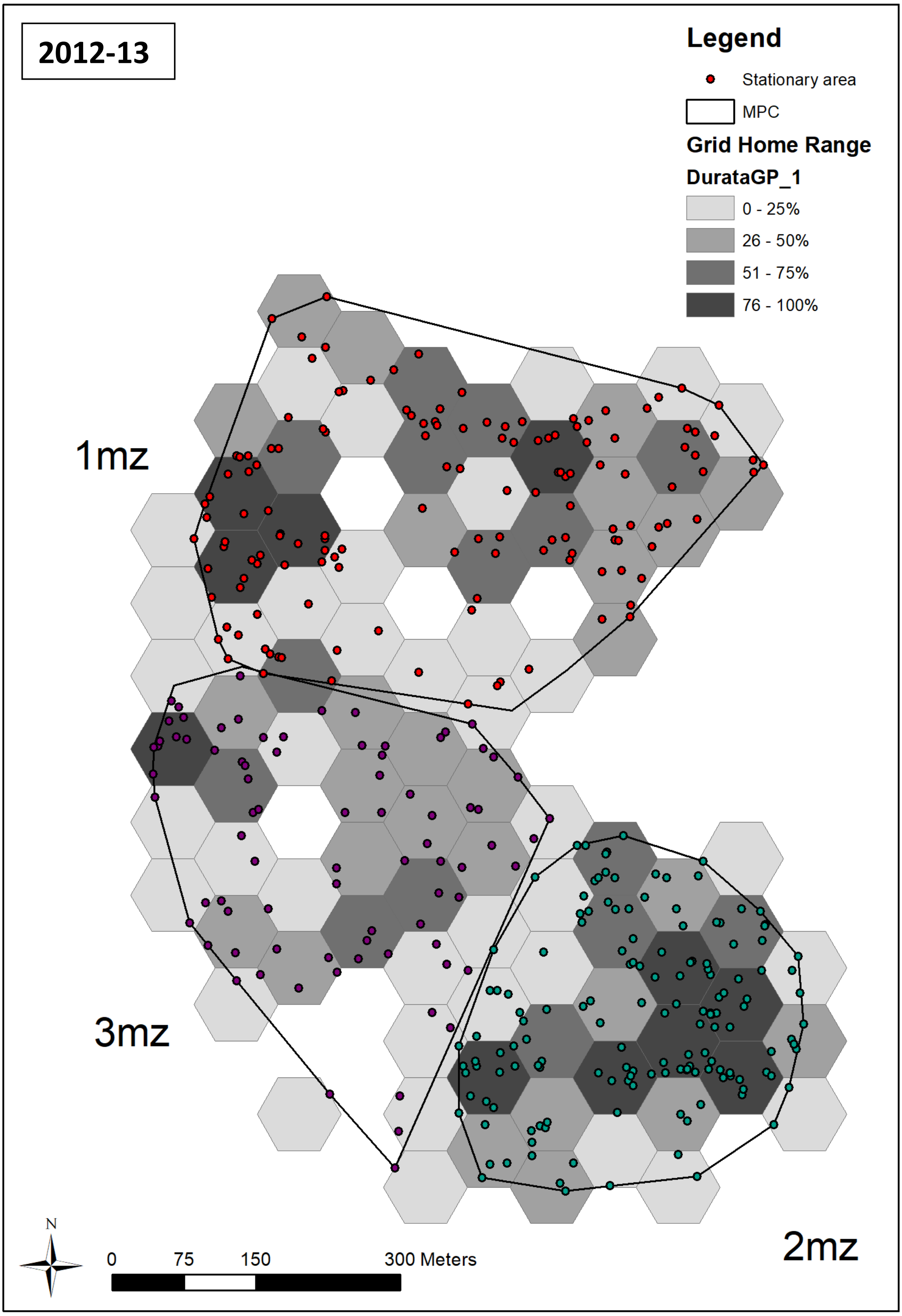
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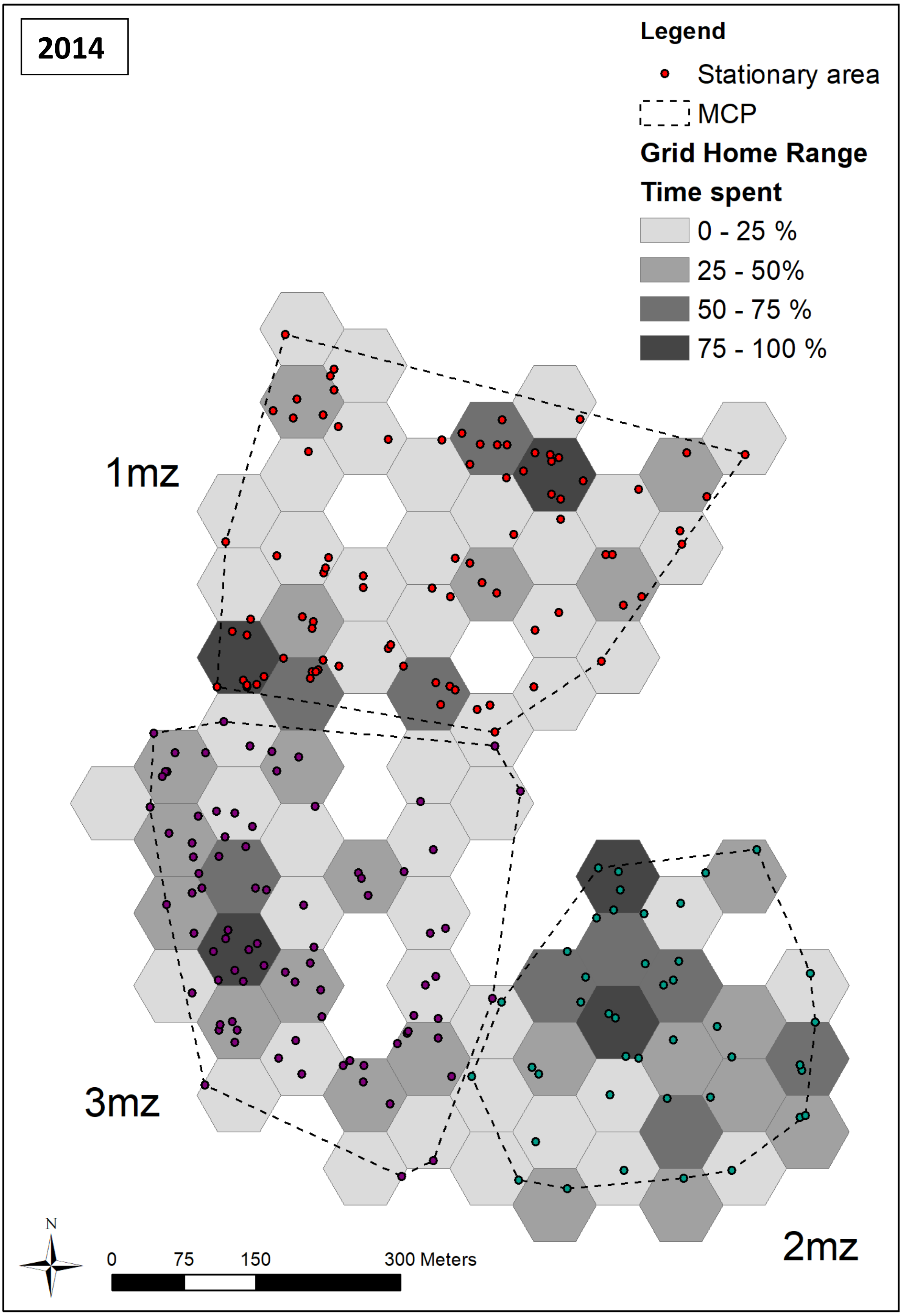
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Intra and intergroup spatial dynamics of a pair-living singing primate, *Indri Indri*. A multiannual study on three indri groups in the forest of Maromizaha, Madagascar.

*Giovanna Bonadonna[1], *Michele Zaccagno[1], Valeria Torti[1], Daria Valente[1], Chiara De Gregorio[1], Rose Marie Randrianarison[2], Chia Tan[3], Marco Gamba[1], and Cristina Giacoma[1]

*joint first authors

[1]Department of Life Science and Systems Biology, University of Turin, Torino, Italy

[2] GERP (Group d'Étude et de Recherche sur les Primates de Madagascar), Antananarivo, Madagascar

[3] LVDI International, San Marcos,CA, USA

Corresponding author: Giovanna Bonadonna

Via Accademia Albertina 13, 10123 Torino, Italy

Phone number: +39 (011) 670 4559

E-mail: bonadonnagiovanna@gmail.com

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

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

Supporting Information: Estimates of territory size obtained with the method of the grids and Minimum Convex Polygons (ESM1), the complete dataset used to conduct the analysis on the core extensions and stability (ESM2), and the map showing core areas overlap between two following sampling periods for each group (ESM3) are available online.

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

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Abstract

Territorial pair-living species tend to occupy stable, defended areas, assumed to contain the totality of resources needed for the lifetime of the social unit. Furthermore, groups have to mediate spatial relationships with neighboring groups. Through the analysis of territorial stability, core areas, and territorial advertisement and defense across time, the goal of this study is to investigate the relationship between social and spatial dynamics at the intra and intergroup level in a pair-living territorial singing primate: the indri (*Indri indri)*. In this study we collected spatial data on three neighboring groups during 396 sampling days between 2009 and 2014 in the 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 resulted to be stable in location and size, although we found that limited territorial shift can occur and lead to intergroup spacing readjustment. Groups have core areas with low stability across years and are concentrated in the area of the territories consistently occupied by groups over time (stable areas). Singing locations were equally distributed within and outside core areas, suggesting an even distribution through the territories; meanwhile 60% of twelve intergroup encounters took place in the core areas and were located at the periphery of territories. Together, our results confirm the pattern of territorial stability expected in a pair-living species, where individuals regulate territory exclusivity and spacing between neighboring groups. The singing behavior also plays an important role in mediating intergroup spatial dynamics. The spatial pattern we found in indris is comparable with the one found in other territorial and pair-livings primates, but with different ecological needs, suggesting that social dynamics can influence intergroup spatial dynamics.

Keywords: intergroup spacing, territorial stability, core area, song spatial distribution, indri

Introduction

Animals adjust their spatial distribution by balancing among their competing demands such as feeding, defending resources, reproducing, dealing with the presence of neighboring individuals or groups and avoiding predators (Waser and Wiley 19779, Lazaro-Perea 2001, Beyer et al. 2010).

The area where animals range to meet their survival needs is referred to as a home range (Burt 1943). A 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 & Lott 1995). When groups defend and exclusively occupy their entire home range, territory and home range coincide (Burt 1943). In the case of territorial species, animals exhibit aggression towards conspecifics attempting to enter a territory (Grant et al. 1992). The strategies of territorial advertisement and defense may influence space use in order to maintain the exclusive access to resources (Brown and Orians 1970, López- Sepulcre and Kokko 2005).

The degree of overlap between territories is the result of an adjustment of space use over time 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, this special issue). 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, this special issue), requiring a consideration of social systems in territorial species.

Previous research has shown that in several species, and across different orders, pair-living is superimposed on a territorial model where the pattern of space use is a reflection of mate guarding strategies and reproductive success (distributed in few species among Crustacean, Insects, Annelids, Fishes, Amphibians, and Mammals) (Emlen & Oring 1977, Clutton-Brock 1989, Roberts & Ormond 1992, Lang & Jaeger 2000, Mathews 2002, Park & Choe 2003). Territorial pair-living species tend to occupy a stable defended area that is assumed to include the totality of resources needed for survival and reproduction in the long term (Börger et al. 2008). Previous findings suggested 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 on territoriality, because it can ensure a limited investment in the interactions with neighboring conspecifics (Bartlett et al. 2016).

Studies on non-human primates have shown that when the habitat is not homogeneous, or that resources are not evenly distributed in space and time, the 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 a more common case for folivorous species, such as gorillas (G*orilla gorilla beringei*) (Watts 1998.a), although they tend to limit the foraging costs by balancing the intensity of use of an area with the regeneration of food resources (Watts 1998.b).

The stable occupation of an area doesn't imply an even use of the space therein, on the contrary, the intensity of use of certain areas depends on resources distribution and interactions with conspecifics or neighboring groups. Group-living primates may tend to use more intensively, certain areas of their range, where they concentrate activities such as resting, feeding, and social behaviors (Bates 1970). Such regions are defined as core areas, and they are considered to have important biological functions for individuals' survival (Burt 1943, Samuel & Green 1988, Asensio et al. 2014). Core areas do not necessarily coincide with the geometrical center of the range; indeed, areas more intensively used can be located on 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 necessity of territorial defense (Vander Wal and Rodgers 2012, Asensio et al. 2014).

The concept of a core area is different from the concept of a territory because the two are based on different assumptions as we intend them: a core area is defined in terms of intensity of use, meanwhile 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 non-defended 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 our study, we identified the core areas as the smallest area of the territory in which a group spent at least 50% of the observation time.

On the other hand, groups tend to avoid certain locations, if there is a risk of potentially dangerous intergroup encounters (Wrangham et al. 2007). For example, in the case of Javan gibbons (*Hylobates moloch*), individuals - especially males – select sleeping sites away from the location of encounters (Yu et al., this special issue), and capuchin monkeys (*Cebus capucinus*) tend to reduce the risk of encounters by avoiding shared or peripheral areas of territories or home ranges (Torrez, this special issue).

A strategy to reduce the costs associated to 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 (Pollock 1986, Cowlishaw 1992). The spatial responses to neighboring loud calls can also be influenced by groups' relative dominance and resources availability, as this has been found 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 grey-cheeked mangabeys, long distance calls can influence the movements of resident individuals with respect to feeding resources (Brown, this special issue).

Because loud calls are a type of signal that can travel long distances, the broadcasting location in a relatively small territory is not a limiting factor in communicating with neighboring groups. Groups can advertise the occupancy of a territory and regulate intergroup spacing without the necessity to concentrate loud calls on the boundaries. Indeed, when the function of the call is to advertise territory occupancy and defensive potential, loud calls tend to be spread within a territory, as per the model of regular advertisement of occupation (da Cunha & Byrne 2006).

The indri (*Indri indri*) is a pair-living primate that lives in family groups. Each group is composed of two to six individuals, consisting of the 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 (EPC) has been reported between two reproductive individuals of neighboring groups (Bonadonna et al. 2014). Individuals pair for years, most reproductive pairs have been together since the habituation in 2009, although rare cases of take-over or new pairing following the death of the partner have been reported for this species (Bonadonna et al. 2019).

Both sexes disperse in this species, and in the population studied in Maromizaha, the offspring remains with the family group for four years, on average (unpublished data). Each group’s range is an exclusive and defended area; the home range coincides with the territory and the overlap between neighboring territories is almost absent. The ranging pattern doesn’t indicate a constant patrolling of the boundaries and groups take approximately two weeks to range in the whole territory, requiring at least 16 days of observation to reach an accurate estimate of territories size (Pollock 1986, Bonadonna et al. 2017).

To communicate at inter and intra group level, indris emit songs in choruses that can vary in size ranging from two individuals – usually the reproductive pair – up to five (Torti et al. 2018). The song is a cost-efficient way to communicate on long distances and one of the main functions is to regulate territorial occupancy besides broadcasting individual cues (Gamba et al. 2016, Torti et al. 2017).

Previous studies show that advertisement and territorial songs have different characteristics and can be recognized depending on 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 only emitted when groups are in visual contact on a territorial boundary, they can last five times more than the average advertisement song and individuals' contribution highly overlap (Torti et al. 2013). In this species, intergroup encounters are an infrequent occurrence (on average one encounter every 20 days), restricted to the peripheral areas of the territory (on average within 22 m from the boundaries). In the majority of cases, the encounters are solved with the emission of territorial songs (87% of reported cases) and ~~,~~ rarely, they can involve chasing and physical fights (13% of cases reported) (Bonadonna et al. 2017).

This study wants to investigate the relationship between social and spatial dynamics in a pair-living territorial primate, and if ~~if a~~ differential intensity of space use within a territory can be 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 on intergroup dynamics over time. In this study, we aim to extend previous findings on the spatial behavior of this species (Bonadonna et al. 2017) thus investigating: (i) the stability of the territories across time, (ii) the presence and stability of core areas over time, (iii) the spatial distribution of singing locations and intergroup encounters within the territories (core areas vs. non-core area).

We hypothesize that indris would show a pattern of territorial stability similar to those found in other pair-livings territorial primates, and that over time the pattern should reflect the history of spatial dynamics between groups, with a tendency to maintain high territorial stability to reduce the costs associated with spatial mediation between neighboring groups (Wartmann et al. 2014, Bartlett et al. 2016, Fernandez-Duque 2016, Van Belle et al. 2018). Therefore, we predict that indri groups might occupy the same area across successive periods with a limited territorial shift.

In the case of folivorous species - such as the indri - food resources are constantly available and not patchily distributed (Milton and May 1976), previous studies on indris' diet found that immature foliage (preferred food item) are available all year around (Powzyk and Mowry 2003). In the prediction of site fidelity, a territory should contain the resources needed in the long term, and core areas are assumed to contain important resources for survival. However, ecological needs might not be the only drivers in the pattern of space use and groups may spend more time in certain areas in response to territorial dynamics and the necessity of territory exclusivity (Asensio et al. 2014).

Because indris require long-term preferred food resources availability, and they regulate territorial dynamics without an intense patrolling of the boundaries, we expect that indris would have core areas that are not stable in successive years with low values of overlap over time, shifting areas intensely used within territories according to availability of food resources and territory exclusivity.

The costs given by the interactions with neighboring groups play a role in the spatial dynamics of a species. In the indri, the overlap between territories is extremely low, the intergroup encounters are at medium risk of aggression (Wrangham 2007, Koch et al. 2016) and are restricted to the peripheries of territories (Bonadonna et al. 2017). Hence, we expect to find higher intensity of use within areas constantly occupied by groups across years, and that peripheral areas might be affected by contentions between neighboring groups.

Previous studies suggested that indris' calling has an effective distance that extends up to two kilometers, beyond the range of a single territory (Pollock 1986, Torti et al. 2017), and thus we predict that calling locations would not necessarily reflect a pattern of distribution associated with the core area but they would rather be evenly distributed within a territory, playing a role in mediating the spatial relationship between groups.

Material and 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, center-eastern Madagascar. Maromizaha extends for 1880 ha and comprises primary and secondary mid-altitude (800 -1200 m) tropical evergreen rainforest, with an annual rainfall of 1779 mm and an endemism rate of 77% (Randrianarison et al. 2015). This kind of forest is a formation characterized by a single stratum from 20 to 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. This study includes spatial data collected on three habituated indri groups (1MZ, 2MZ, 3MZ) (Table1).

Table 1. Data set description. For each group, we provided group size and composition (af/am: adult female and adult male, sam/saf: sub-adult male and female, jf/jm: juvenile female and

male; j: juvenile sex unknown) total number of locations recorded for that study period, the number of sampling days and months of data collection.

Group code	Study periods periods	Group size	Group composition	Total # locations recorded	Total days of sampling	Sampling months
1MZ	2009-2010	3	af, am,sam	107	29	Dec 2009 Apr; Oct-Dec 2010
	2011	4	af, am, sam, jf	122	30	Sept-Dec
	2012-2013	4	af, am, saf, jf	141	45	Jan-Feb; Apr-Oct; Dec 2012
	2014	3	af, am, jf	86	32	Feb-Apr; Jun-Sept
2MZ	2009-2010	3	am, af, j	109	33	Nov-Dec 2009 Mar; Oct-Dec 2010
	2011	2	am, af	90	23	Aug-Dec
	2012-2013	2	am, af, jf	150	45	Feb; Apr-Dec 2012 Feb-Mar 2013
	2014	3	am, af, saf	42	17	Feb-Sep
3MZ	2009-2010	4	am, af, sam, jf	128	40	Nov-Dec 2009 Feb-Mar; Oct-Nov 2010
	2011	4	am, af, sam, jf	149	38	Aug-Dec
	2012-2013	3	am, af, saf	83	30	Apr- Jul; Sept-Dec 2012 Feb-Mar 2013
	2014	4	am, af, saf, jm	84	34	Feb-Sept
Total				1291	396	

Data Collection

We collected data on the three focal groups during four study periods, between 2009 and 2014 (Table 1). For the years 2009 and 2013 we did not have a dataset robust enough for all the three groups to analyze the study periods separately (Bonadonna et al. 2017). Because we wanted to investigate spatial dynamics across time, we prioritized the continuity for each study period, avoiding the loss of biological information. Therefore, we joined the data collected during November and December 2009 with 2010, and the data collected in February and March 2013 with 2012.

Given the indris' diurnal habits (Pollock 1975), we started observations early in the morning, at about 06:00, when individuals begin to be active, and we followed groups until they became inactive at about 13:30. Individuals were identified by the pattern of fur patches and were not radio-collared.

We recorded the location of the center of the group members by using a hand-held global positioning system (GPS Garmin MAP 76CSX), with an accuracy of at least five meters. A previous study on indris' spatial behaviour (Bonadonna et al. 2017), showed that their ranging pattern is characterized by progressive directional displacements, and a group needs about 2 weeks to patrol the entire territory by visiting a minimal part of this each day. We consistently followed the methodology shown in that previous study, by recording a new GPS point each time the animals reached a new location after having interrupted their previous activities, and had moved at minimum 20 m from the previous location (see 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. On average, groups visited three stationary areas per day of observation (Table 1). This protocol, based on biological relevance rather than arbitrary time intervals between recorded locations, allowed us to avoid autocorrelation between points still maintaining biological information. We included in the analyses all waypoints recorded during the days of focal observations.

Every time the focal group emitted a spontaneous advertisement song or was involved in intergroup encounters during the focal observations (Torti et al. 2013) we noted the geographical coordinates of the corresponding location. No playback responses that could bias the singing locations were included in the study. All the field operators followed the same protocol, including researchers and trained research guides that contributed to data collection.

Spatial and Statistical Analysis

All spatial data were analyzed in ArcGIS 9.3 or ArcGIS 10.1 (ESRI 2012). We calculated the linear extension of the territories using Minimum Convex Polygon (MCP) 100% since 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). All the statistical tests were performed in IBM SPSS 22. The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Territory Stability

We investigated the degree of stability of the 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 shift of the geometric centroids of a territory between consecutive study periods. We reported the size of territories in hectares (ha) for each study period, and we calculated the size variability as the absolute value of change in percentage of territory size between two consecutive study periods. To describe the extent of variability of the territories 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 on territories and home range stability in primates (Janmaat et al. 2009, Asensio et al. 2012, Bartlett et al. 2016). 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 0-33% are classified as low overlap, 34-66% as moderate overlap, and 67-100% as high overlap (Kernohan et al. 2001). We also reported 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 2000). We then calculated the linear distance (m) between centroids observed in two consecutive periods.

Core area designation and stability

In our dataset, the time spent by a group in each recorded GPS waypoint may vary, depending on how long a group remained in a stationary area. Hence, in our dataset the number of waypoints itself does not reflect the intensity of use of an area. To indicate the differential intensity of use within each territory, we created a grid with hexagonal cells of .50 ha each, by using the ArcGis extension Patch Analyst (Rempel and Kaufmann 2003; Asensio et al. 2012). By summing the minutes spent at each waypoint included in a cell, considering only cell grids in which the stationary area centroids are contained, we obtained the cumulative time spent at each hexagon by a group.

To evaluate a differential intensity of use throughout the territory, we identified four classes of intensity of use of each cell based on the minutes spent in each hexagon by using ArcGis to classify them. To standardize the different times among groups, we set between 0 and 100% the minimum and maximum time spent for each group in a cell and set break values at interval of 25%. We obtained a map showing a gradient intensity of use throughout the territory, Electronic Supplementary Material 1 (ESM1) reports the territory size calculated with the method of the hexagonal grid for comparison purposes.

Afterwards, we ordered the cells according to their time values, and we manually 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 represents the core area. We excluded a potential correlation between the percentage of territory representing the core area and absolute territory size by running a Pearson's correlation (Pearson's correlation: 0.1, P=0.656, N=12). Because the sampling span is not homogeneous across study periods, we tested with a Spearman's Rho an eventual correlation between the sampling effort as number of months per study period and the size of the core areas, however we did not find a significant correlation (Spearman's Rho: rs = 0.4, P=0.227, N=12).

To estimate the stability of the identified core areas across study periods, we overlapped yearly core areas obtaining the regions consistently maintained as core area across time (overall stable core area) and quantified the parameters of size variability between years and the Minta Index, both calculated as previously described for the territory stability. We reported the extent of core area shared between two consecutive periods for each group, calculated as percentage of core area maintained from the previous year; we obtained the proportion of core area included within the territory in two consecutive years by calculating the percentage of core area included in the MCP of the consecutive study period. Finally, we reported the percentage of core area included in the overall stable area of territories.

Spatial distribution of singing locations and intergroup encounters

We recorded a total of 191 singing locations for the three groups during the entire study: 77, 64, and 50 for the groups 1MZ, 2MZ, and 3MZ, respectively. We plotted the singing locations recorded during a study period on the respective annual core area for each of the three indri groups, then we 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 cumulative frequencies of singing location inside and outside the core areas for each group. We performed a Chi-squared test of goodness-of-fit ($\alpha \leq .05$) to compare the frequency of singing locations between core and non-core areas; we defined expected values, considering the null hypothesis of an even spatial distribution of singing locations, given the fact that the groups spent half of the observation time inside or outside the core areas, according to our definition.

We recorded a total of twelve intergroup encounters over the entire study period, four for each group, and we took note if encounters were solved through the emission of territorial songs or if they involved physical fights. We plotted the encounters in the territories, and we reported the percentage located in the core areas; we also counted how many of the encounters were located in the overall stable area of territories. To account for movements of the groups during intergroup encounters, we applied a 20 m buffer (10 m radius) to each encounter point.

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'Etude et de Recherche sur les Primates du Madagascar). During observations, we followed the groups at a distance of 10–50m, avoiding any unnecessary disturbance. All the groups studied were 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 eco-tourism. None of the field operators got 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 the research permits for the field activity 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).

Results

Territory Stability

The map showing the overlapping annual MCPs indicates that the three groups tended to have stable territories across the study period (2009 – 2014) (Fig. 1A). The results are consistent across all the three parameters considered: size variability, intra-group territory overlap, and centroid shift, even if we observed some degree of flexibility among the groups' territories (Table 2 and Table 3).

Size variability

We found an overall mean territory size of 12.7 ± 2.8 ha (N=12), ranging between 9.2 and 17.5 ha (with the method of the grid we obtained an overall average territory size of 16.0 ± 2.5 ha (N=12), ESM1). The overall mean difference in territory size between two consecutive study periods is 10.6 ± 5.5 % (N=9), ranging between 13-22% for group 1MZ, 4-7% for group 2MZ, and 8-12% for group

3MZ. Group 1MZ showed the greatest increase in territory size over time , group 2MZ had the smallest and most stable territory across years , and group 3MZ was intermediate both in terms of territory size and stability over time compared to other two groups (Table 2). The CVs show a comparable variability in territory size across years among groups (Table 2).

Intra-group territory overlap

According to the Minta Index, we found that the groups 1MZ and 2MZ show high overlap of their territories across time, and group 3MZ is at the upper limit of medium overlap (Table 3). The overall mean percentage overlap between the MCP of a given study period and the overall stable area was 63.9 ± 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 2) indicating higher flexibility in annual territory overlap with the overall stable area. Except for the group 3MZ, the degree of territory overlap between consecutive study periods increased over time (Fig. 2A).

Centroid shift

The centroids showed little shift over time with an overall mean of 32m ±24 (N=12), ranging between 2 m (group 1MZ) and 82 m (group 3MZ). The average shift of centroid between two consecutive periods was 14 ±11 m (range: 2 - 22 m) for group 1MZ, 32 ± 19 m (range: 15 – 53 m) for group 2MZ, and 50 ± 28 m (range 34 – 82 m) for group 3MZ (N=3 for each group). We found the greatest shift of centroids for the group 3MZ between 2010 and 2011, which reflects the lowest values of inter-annual territory overlap found for this group (Fig. 2A). During the same interval of time, we observed a 53 m shift of centroid, the second largest, for the adjacent territory occupied by the group 2MZ (Fig. 1A).

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

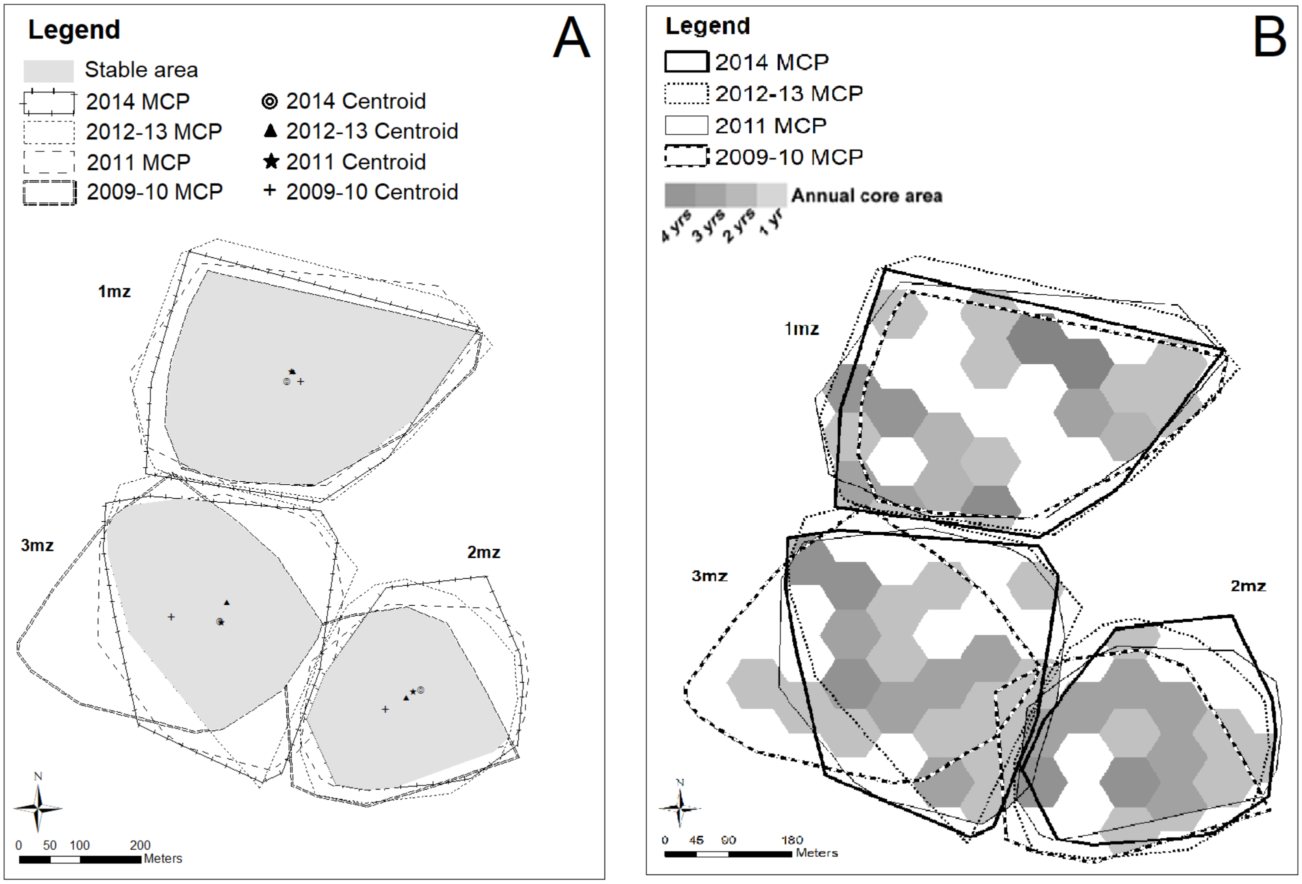


Fig. 2. Territory and core area overlap for the indri groups 1MZ, 2MZ, 3MZ over four study periods (2009-2014) in the Maromizaha forest, Madagascar. Lines indicate the inter-annual variation for each group. The star (*) indicates a study period comprising two different years (e.g. 2010* comprises both 2009 and 2010). A. Intragroup territories 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 percentage in relation to the total extension of the consecutive study period. In D. overlap is expressed as percentage in relation to the core area total extension, within the same study period.

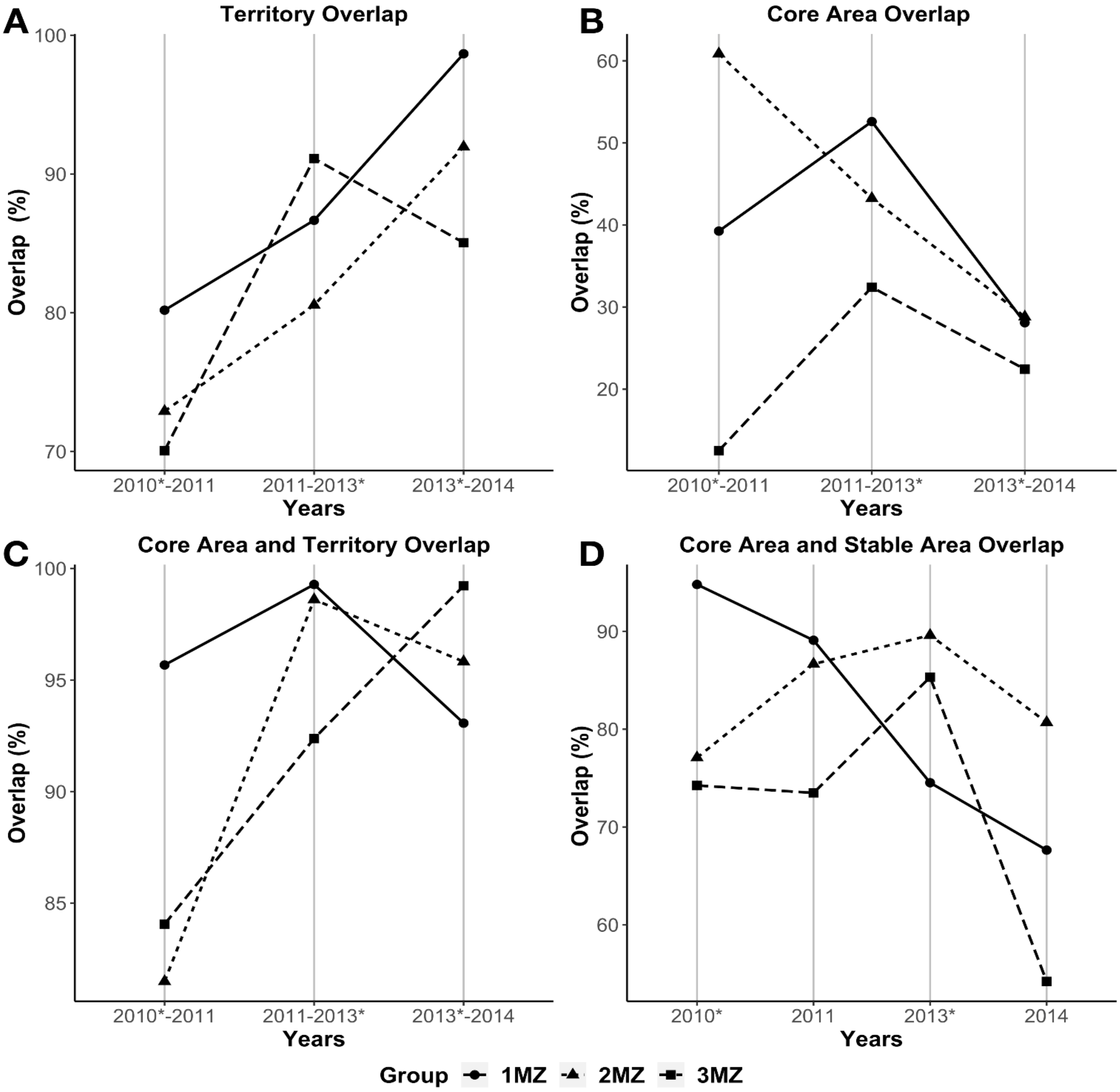

A
Territory Overlap
Overlap (%)
100
90
80
70
2010*-2011
2011-2013*
2013*-2014
Years
B
Core Area Overlap
Overlap (%)
60
50
40
30
20
2010*-2011
2011-2013*
2013*-2014
Years
C
Core Area and Territory Overlap
Overlap (%)
100
95
90
85
2010*-2011
2011-2013*
2013*-2014
Years
D
Core Area and Stable Area Overlap
Overlap (%)
90
80
70
60
2010*
2011
2013*
2014
Years
Group
1MZ
2MZ
3MZ

Table 2. Territory and core area size and stable area. Territory and core area size for each indri group in each sampling period and the respective mean, standard deviation (SD), and coefficent of variation (CV). The table includes the area constantly occupied by a group across sampling periods (overall stable area) for territories and core areas, respectively.

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

Table 3. Terriotry and Core Area Overlap with Respective Overall Stable Area and Minta Indices. 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 sampling 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).

Study period	Overlap MCP- overall stable area (%)			Overlap CA - overall stable CA (%)		
	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

Intensity of Use and Core Area

We found that areas at higher intensity of use can have a scattered distribution through a group's range and can be located in the center as well as in more peripheral areas of a territory. The same is true for the areas less intensely used by a group in a given year (Fig .3).

Quantifying the size of the core area for all the groups for all study periods, we determined that the groups spent 50% of their time in a mean area of 3.4 ± 0.8 ha (N=12), with the core area representing 26.7 ± 4.7% (N=12) of the territories (ESM2). Considering each group separately across the four study periods, we found that the core area represents 24.0 ± 4.4% (N=4) of the territory for the group 1MZ, 29.0 ± 5.1% (N=4) for the group 2MZ, and 27.1 ± 4.1% (N=4) for the group 3MZ. Core areas of neighboring groups never overlapped during a study period, although they could be adjacent to each other (Fig. 4).

We found considerable variation in core area size and location across time. Core area sizes ranged between 2.7-4.8 ha for the group 1MZ, 2.2-3.5 ha for the group 2MZ, and 2.9-4.2 ha for the group 3MZ (Table 2). We found a greater change of core area size between study periods compared to the variability found for territory size, with an overall mean change of 22.2 ± 18.7 % in size between consecutive study periods (N=9). The high CVs indicate that the core area size of a group can greatly vary from a year to another (Table 2).

Fig 3. Intensity of use. The territories of three indri neighboring groups in four study periods between 2009 and 2014 are shown. The outlines represent the Minimum Convex Polygons (MCP). Different shades of gray represent the intensity of use in terms of time spent in a cell by a group as percentage of the total time of observation. The lined pattern indicates overlapping cells between groups.

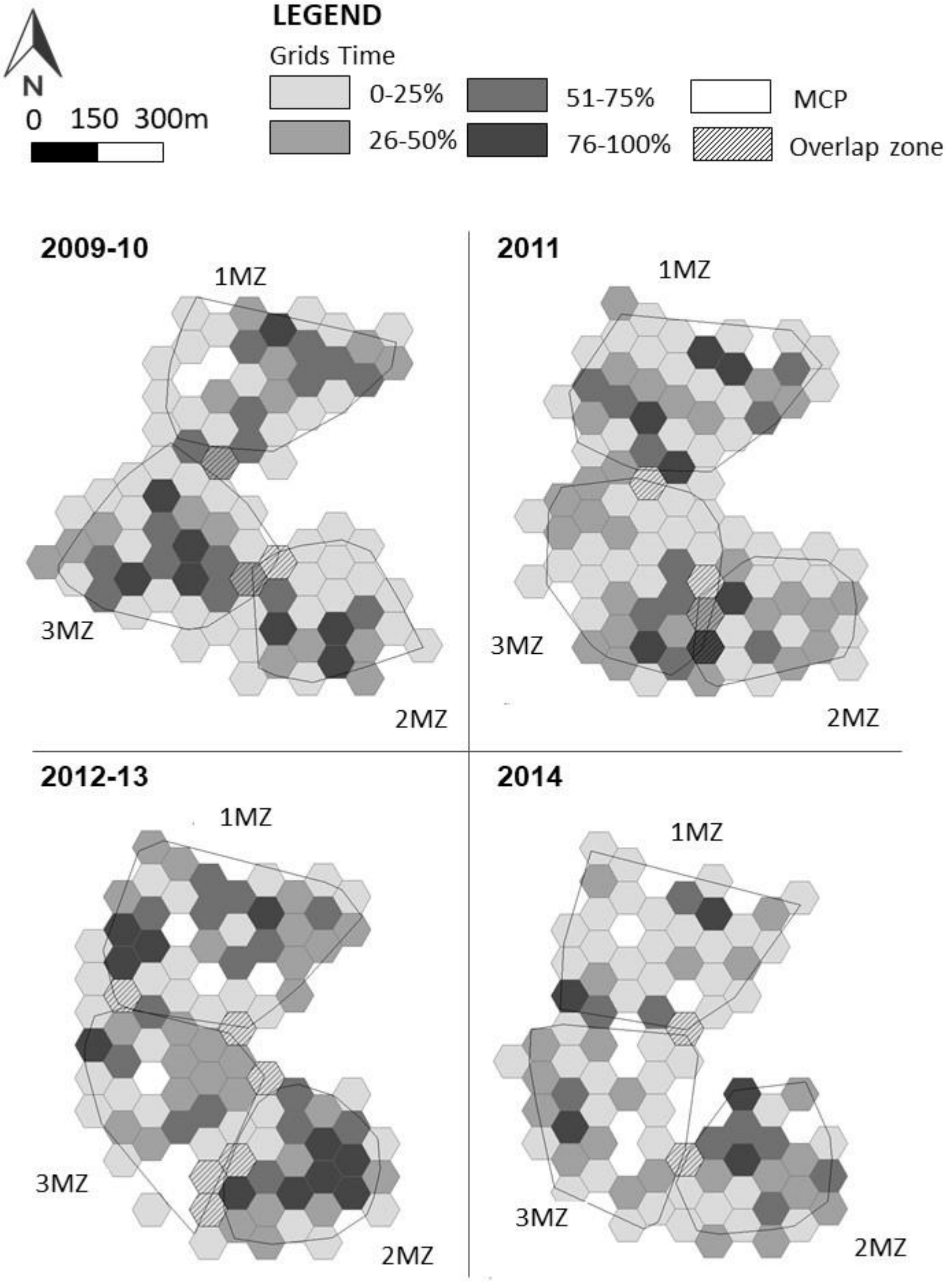
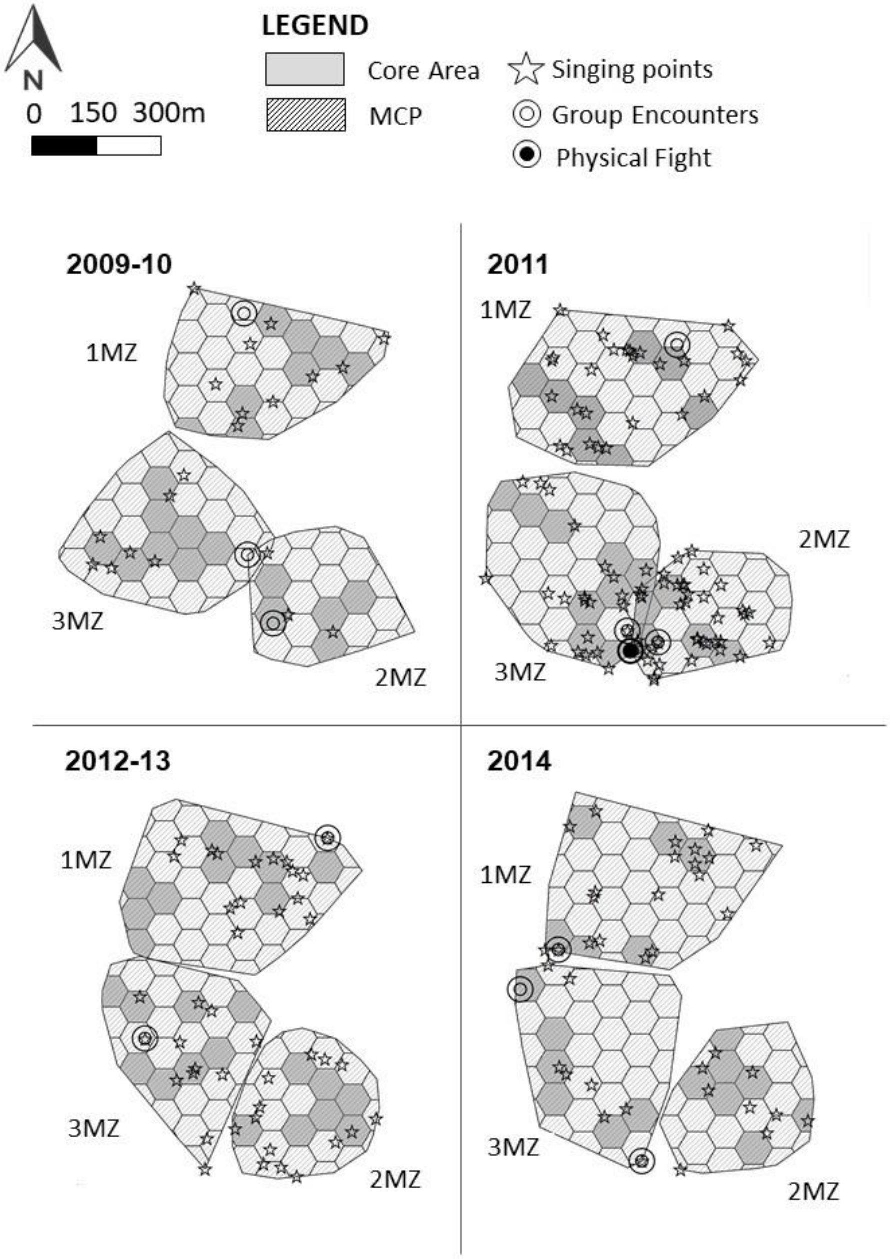


Fig. 4. Core Area, spatial distribution of singing locations and intergroup encounters of three indri neighboring groups in Maromizaha, Madagascar, during four study periods.

Spatial distribution of core area (gray cells), singing location (stars), and intergroup encounters (circles) in each indri territory (MCP) during four study periods between 2009 and 2014 (each box represents a different period). The encounters include a 10 m radius buffering area. The black dot marks the only intergroup encounter that involved a physical fight besides the emission of territorial songs (2011).



All three indri groups exhibited low overlap of core areas across years (Table 3). The only group presenting core area overlap throughout the four study period was 1MZ; even if they occupy a smaller territory than the group 1MZ, neither group 2MZ nor 3MZ had an overall stable core area (Table 2 and 3). When considering the overlap of core areas between two consecutive study periods, we found a certain degree of intersection for all the groups (ESM3). Group 2MZ showed the highest percentage of core area overlap between two consecutive periods (61%), although decreasing over time. Meanwhile, the groups 1MZ and 3MZ showed a similar pattern of overlap between two years over time, with group 3MZ presenting the lowest values, ranging between 13% and 32% (Fig. 2B). Considering the distribution of core areas within a territory, we found an overall mean of 93.3% ±6.5% (N=9) of core areas 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 indri groups presented a general increasing trend with the last period presenting overlap values over 95% (Fig. 2C). Across the study period, we found that on average 78.9 ± 11.2 % (N=12) of core areas are located in the overall stable area, ranging between 95.8% (group 1MZ) and 54.2% (group 3MZ) (Fig. 2D).

Spatial distribution of singing locations and intergroup encounters.

Fig 4 shows the spatial distribution of the singing locations and intergroup encounters within the territories of the focal groups in a given study period. On a total of 191 singing locations recorded, 98 were inside the core areas. Considering the cumulative number of singing locations for each group, we obtained a mean proportion of 55.9% ± 5.2 (N=3) of songs emitted from the core areas. We did not find a significant difference in the frequency of singing locations distribution between core and non-core areas for any of the three groups: for group 1MZ, 37 locations (48.1%) were in the core area (χ^2 (1, n =77) = .117, P=.732); for group 2MZ, 32 locations (50.0%) were in the core area (χ^2 (1, n =64) =

.000, P=1); for group 3MZ we found 29 locations (58.0%) in the core area (χ^2 (1, n =50) = 1.280, P=.258).

We found that on a total of 12 intergroup encounters, 60% were located in the core areas. All the encounters were solved through the emission of territorial songs except for one encounter between the groups 2MZ and 3MZ in 2011, when the two groups were involved in a physical fight. It is worthy to note that three of the four encounters recorded in 2011 involved the groups 2MZ and 3MZ, following a shift of the territory of group 3MZ toward the East side that resulted in an overlap between the two groups (Fig 4). Figure 4 shows, that 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. It is interesting to note that group 3MZ was in the numeric majority; in 2011 group 3MZ was composed of four individuals including three singers and a two-year-old non-singing juvenile, meanwhile the groups 2MZ was composed of the reproductive pair only after losing their last infant in 2010 (Table 1). Also, in 2011 the female of group 3MZ (Mena) was involved in the Extra Pair Copulation with the reproductive male of the group neighboring on the West side.

Discussion

Our study provides information about the stability of territories and space use over time in the indri. Territories were stable in terms of both size and location over four study periods. Our study confirmed the presence of core areas shifting over time, but remaining part of the territory in successive years, and tending to be concentrated in the stable area of a territory. In particular, we found that there are areas intensively used over a multi-annual span, and others that have never been included in a core area during the entire study period. Our results indicate that none of the three indri groups called more frequently from core areas than the rest of the territory, and that intergroup encounters - although rare - are more frequent in peripheral areas that are also intensively used by a group.

Territory stability

The indri groups showed a degree of site fidelity comparable with 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 2003); 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 (Vander Wal and Rodgers 2012, Bartlett 2015). 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.

According to our results, high stability can be explained as a strategy that limits the costs of spatial competition between groups to keep the exclusive use of the territory and, in a pair-living system, to ensure the exclusive access to the partner. 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 the 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 necessity of territory exclusivity, which is considered a prerequisite in maintaining a pair-living sexually monogamous mating system (Reichard and Boesch 2003). The group with weaker stability (3MZ) was the same involved in the only extra pair copulation (EPC) observed in this species (Bonadonna et al. 2014), suggesting that less territorial stability may coincide with social and reproductive inter-group 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 that we identified as the core area. The intensive use of an 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 for the indri, the portion of territory occupied by a core area is independent of absolute territory size, suggesting a link between size variability of the core areas and the respective territory extension.

We found that core areas shift across years but tend to be included in the territory of the successive year, and across years they cover the whole territory. Similar results have been found in multi annual studies on white-handed gibbons (Hylobates lar) (Bartlett et al. 2016) and on spider monkeys (Ateles geoffroy) (Asensio 2011), although both species are highly frugivorous and a shift of the core areas has been explained with changes in preferred food availability over time (Asensio et al. 2014), the results are in agreement with the importance for territorial species to occupy an area that include future core areas. On the other hand, a long-term study on another population of spider monkeys found that core areas were more stable than home range, probably due to a high fidelity to locations of high-quality habitat (Ramos-Fernandez et al. 2013), suggesting that there can be a patter variation at intraspecific level due to the locations of such habitat (Ramos-Fernandez et al. 2013).

Because of a similar pattern in home range and core area stability between species with different diets, and a different pattern between populations of the same species, we can infer that resources location are surely important in defining space use dynamics over time, but the role of territorial defense and control to mate access in pair-living species is also a contributing factor, as mate location is less predictable than the location of food resources.

Although indris base more than 70% of their diet on young leaves and 16% on fruits (Powzyk and Mowry 2003), we do not exclude that other factors may influence the differential intensity of space use in this species. These factors may be ecological, such as the regeneration of young leaves, or the distribution in space and time of preferred resources, or geographic features of territories (i.e., the presence of rivers and falls or the topography of the territories). Our current data does not allow us to draw conclusions on this point and this hypothesis requires further investigation.

Group dynamics and intergroup encounters

Different studies found evidence that overlapping zones between territories, although limited in size and occurrence compared to non-territorial species, tend to be underused especially when there is the risk to incur in potentially dangerous fights with neighboring groups (Wrangham et al. 2007, Torrez this issue). In agreement with previous findings, the overlap between territories is almost absent in indris (Bonadonna et al. 2017); given the fact that indri groups do not share areas of their territories, it is not surprising that in this species intergroup encounters are rare, 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 border increases the probability to engage in an intergroup encounter, despite the limited or absent overlap between territories. On the other hand, groups may spend more time in areas where an intergroup encounter took place to defend a disputed area of the territory. Furthermore, we found that even if core areas were located in the peripheral area of a territory, they are more concentrated in the overall stable area occupied by a group, suggesting the tendency to concentrate activities in areas less affected by shifts over time potentially contended between groups.

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 the female (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. 2000), while at the same time displaying their ability to defend a territory (Kempenaers and Dhondt, 1993).

A comparison between the rate of intergroup encounters and the mating system in indris and gibbons provides a good example. Intergroup encounters in indris are rare. Previous studies reported only one observation of Extra pair Copulation (Bonadonna et al. 2013) and genetic monogamy seems to be the norm in this species (Bonadonna et al. 2019). On the other end, studies on gibbons showed that they present a high rate of intergroup encounters, and pair-living females are sexually promiscuous with higher rates of extrapair copulation compared to the indris (Reichard and Barelli 2008, Barelli 2013), although intergroup interactions in white handed gibbons are not exclusively agonistic (Bartlett 2003).

Singing locations

We found that the indri's advertisement songs are equally distributed inside and outside the core areas, relative to the time spent by a group in those areas. The fact that core areas shift over time can justify the strategy to advertise groups' presence throughout their territories rather than concentrate the advertisement in areas more intensely used in a relatively short term. Indris groups emit on average 2.2 advertisement songs per day (Torti et al. 2013) and the signal can reach far beyond the territory extent, eliminating the necessity 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 in indri in maintaining territory occupancy (Pollock 1986, Geismann and Mutcschler 2006), reducing the necessity of incurring in more costly intergroup confrontations. This description fits with the model of regular advertisement of occupation, which predicts the spread spatial distribution of loud calls within a territory when they have the function of signaling 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 gibbons (*Hylobates klosii*) most of the post-dawn singing locations are placed in what the authors call "most used area" (Whitten 1982). On the other hand, the spatial distribution of territorial songs (emitted exclusively during intergroup encounters) is limited to the boundaries, fitting with the model of territorial boundary marking and defense (da Cunhna and Byrne 2006) and in accordance with the proximate cause of territorial songs previously proposed for this species (Torti et al. 2013). In conclusion, we believe that given the pronounced territoriality of this species, and the efficient spacing regulation between neighboring groups, the pattern of space use in indris is influenced by intergroup dynamics and that vocal communication plays an important role.

It is recognized that the maintenance of stable and exclusive territories, as we found for indri, is a prerequisite for the evolution and maintenance of a pair-living 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 strictly bound may require the evolution of strategies to regulate communication and relationship at the inter-unit level, because units compete and are not independent of each other (Fuentes 2000, Tsai 2002, Bartlett 2003, Furuichi this special issue).

From their studies on white handed gibbons, Bartlett and colleagues (2016) suggested that social factors can also drive space use besides ecological factors, and that to better understand the behavioral ecology of a species, social units should not be considered independently but as part of a network. We found a similar pattern in the indri, a species with a different feeding ecology when compared to gibbons, but with many similarities in their social organization and vocal communication. However, the relevance of the link between the social organization and mating system with external and ecological factors is an idea that has been suggested decades ago (Tsai 2002, Bartlett 2003). Further studies on the spatial and temporal distribution of preferred food resources are needed to have a more complete understanding of the role of ecological variables in the differential intensity of use within an indri territory over time.

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Conflict of interests

The authors declare that they have no conflict of interest.

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