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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--Manuscript Draft--

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

Changed, thank you.

Added, thank you

We changed groups with groups'

Noted, thank you.

Changed, thank you.

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.

Corrected, thank you.

We deleted the second half of the sentence.

Changed, thank you.

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.

<mark>Line 166 - add "of" after "loss"</mark>
Added, thank you

<mark>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).</mark>

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.
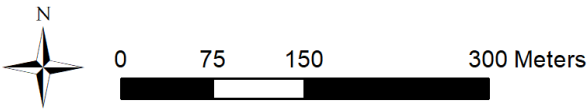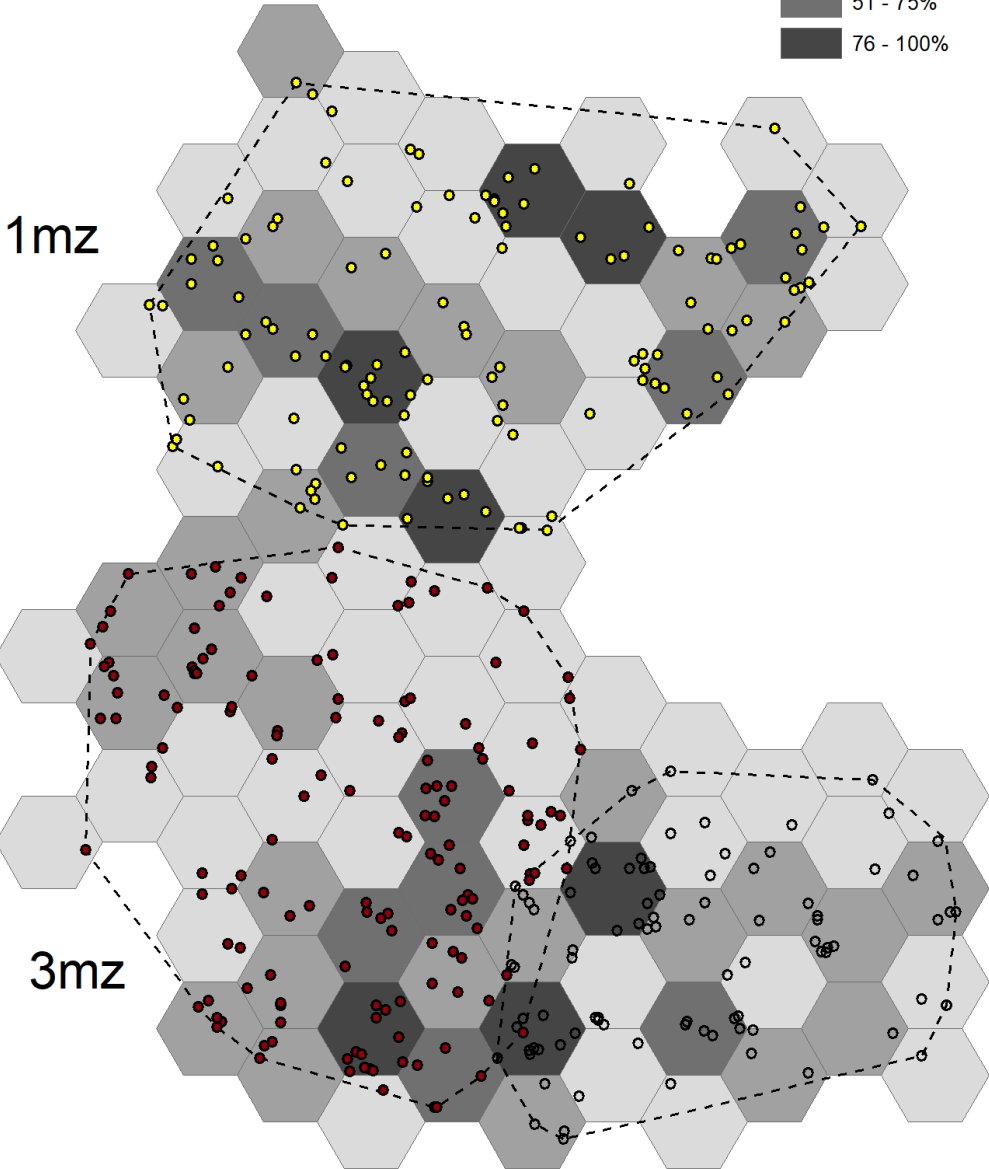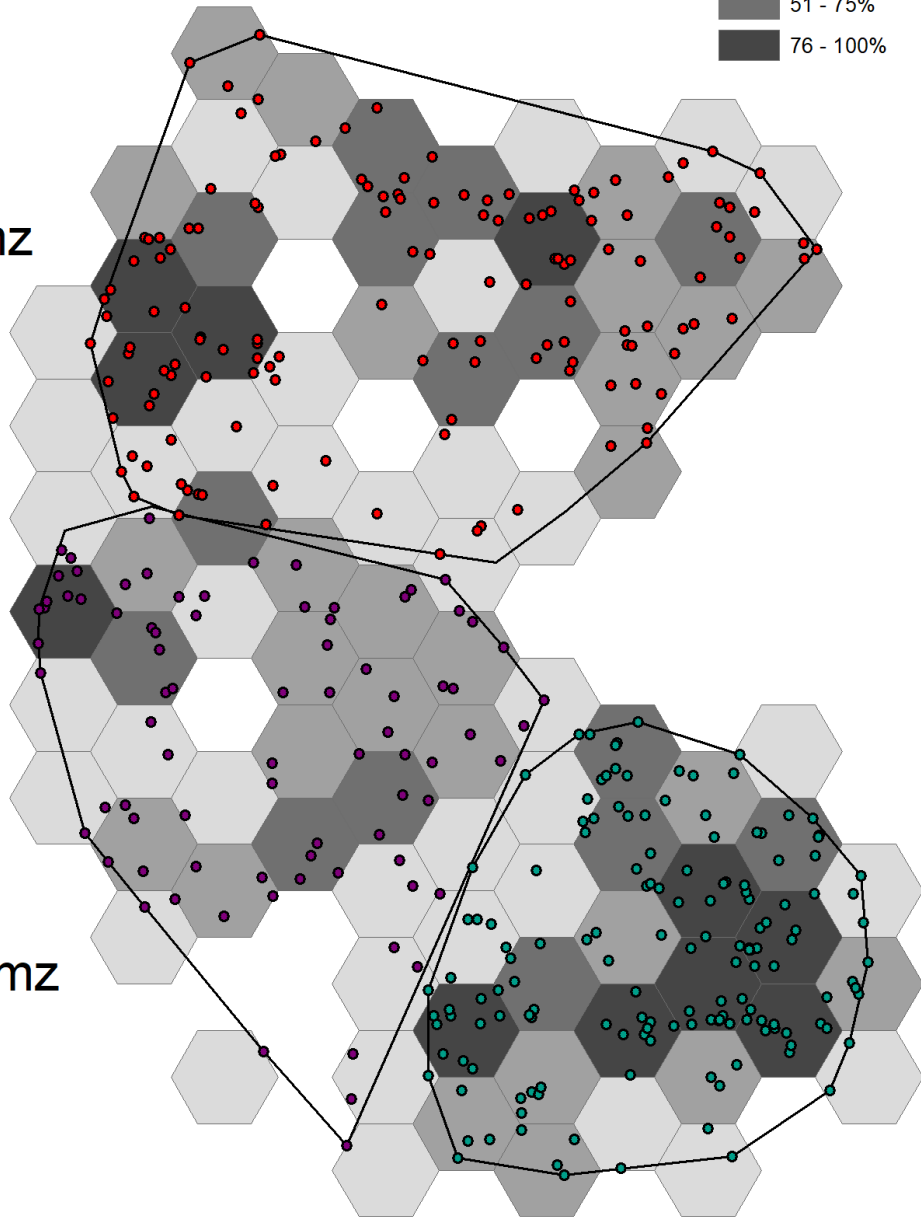
1   **Intra and intergroup spatial dynamics of a pair-living singing primate, *Indri Indri*. A**

2   **multiannual study on three indri groups in the forest of Maromizaha, Madagascar.**

3

4   *Giovanna Bonadonna[1], *Michele Zaccagno[1], Valeria Torti[1], Daria Valente[1], Chiara De Gregorio[1],

5   Rose Marie Randrianarison[2], Chia Tan[3], Marco Gamba[1], and Cristina Giacoma[1]

6   *joint first authors

7   [1]Department of Life Science and Systems Biology, University of Turin, Torino, Italy

8   [2] GERP (Group d'Étude et de Recherche sur les Primates de Madagascar), Antananarivo, Madagascar

9   [3] LVDI International, San Marcos,CA, USA

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11

12   Corresponding author: Giovanna Bonadonna

13   Via Accademia Albertina 13, 10123 Torino, Italy

14   Phone number: +39 (011) 670 4559

15   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.

38   **Supporting Information**: Estimates of territory size obtained with the method of the grids and

39   Minimum Convex Polygons (ESM1), the complete dataset used to conduct the analysis on the core

40   extensions and stability (ESM2), and the map showing core areas overlap between two following

41   sampling periods for each group (ESM3) are available online.

1 **Intra and intergroup spatial dynamics of a pair-living singing primate, *Indri Indri*. A**

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3 **Abstract**

4 Territorial pair-living species tend to occupy stable, defended areas, assumed to contain the

5 totality of resources needed for the lifetime of the social unit. Furthermore, groups have to mediate

6 spatial relationships with neighboring groups. Through the analysis of territorial stability, core areas,

7 and territorial advertisement and defense across time, the goal of this study is to investigate the

8 relationship between social and spatial dynamics at the intra and intergroup level in a pair-living

9 territorial singing primate: the indri (*Indri indri*). In this study we collected spatial data on three

10 neighboring groups during 396 sampling days between 2009 and 2014 in the Maromizaha forest,

11 Madagascar. We evaluated the stability of territories in terms of size and location using Minimum

12 Convex Polygons, defined the presence and stability of core areas, and investigated if singing locations

13 and intergroup encounters were concentrated in the core areas. Territories resulted to be stable in

14 location and size, although we found that limited territorial shift can occur and lead to intergroup

15 spacing readjustment. Groups have core areas with low stability across years and are concentrated in

16 the area of the territories consistently occupied by groups over time (stable areas). Singing locations

17 were equally distributed within and outside core areas, suggesting an even distribution through the

18 territories; meanwhile 60% of twelve intergroup encounters took place in the core areas and were

19 located at the periphery of territories. Together, our results confirm the pattern of territorial stability

20 expected in a pair-living species, where individuals regulate territory exclusivity and spacing between

21 neighboring groups. The singing behavior also plays an important role in mediating intergroup spatial

22 dynamics. The spatial pattern we found in indris is comparable with the one found in other territorial

23   and pair-livings primates, but with different ecological needs, suggesting that social dynamics can

24   influence intergroup spatial dynamics.

25   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

49 strategies and reproductive success (distributed in few species among Crustacean, Insects, Annelids,

50 Fishes, Amphibians, and Mammals) (Emlen & Oring 1977, Clutton-Brock 1989, Roberts & Ormond

51 1992, Lang & Jaeger 2000, Mathews 2002, Park & Choe 2003). Territorial pair-living species tend to

52 occupy a stable defended area that is assumed to include the totality of resources needed for survival

53 and reproduction in the long term (Börger et al. 2008). Previous findings suggested that a pattern of

54 stable use of an area over time, defined as site fidelity, is due to the predictability of food resources

55 distribution (Asensio et al. 2012, Ramos-Fernandez et al. 2013). Furthermore, the presence of

56 neighboring exclusive territories can limit the shift of territories over time, imposing a system of site

57 fidelity. Consequently, site fidelity has implications on territoriality, because it can ensure a limited

58 investment in the interactions with neighboring conspecifics (Bartlett et al. 2016).

59   Studies on non-human primates have shown that when the habitat is not homogeneous, or that

60 resources are not evenly distributed in space and time, the knowledge of food resource availability and

61 distribution can make site fidelity advantageous (Janmaat et al. 2009, Ramos-Fernandez et al. 2013,

62 Wartmann et al. 2014). Site fidelity appears weaker when food resources are abundant and evenly

63 distributed, which is a more common case for folivorous species, such as gorillas (*Gorilla gorilla*

64 *beringei*) (Watts 1998.a), although they tend to limit the foraging costs by balancing the intensity of use

65 of an area with the regeneration of food resources (Watts 1998.b).

66   The stable occupation of an area doesn't imply an even use of the space therein, on the contrary,

67 the intensity of use of certain areas depends on resources distribution and interactions with conspecifics

68 or neighboring groups. Group-living primates may tend to use more intensively, certain areas of their

69 range, where they concentrate activities such as resting, feeding, and social behaviors (Bates 1970).

70 Such regions are defined as core areas, and they are considered to have important biological functions

71 for individuals' survival (Burt 1943, Samuel & Green 1988, Asensio et al. 2014). Core areas do not

72   necessarily coincide with the geometrical center of the range; indeed, areas more intensively used can

73   be located on the periphery of a territory or home range (Asensio et al. 2014) and can be more or less

74   stable over time depending on the distribution of preferred food resources and the necessity of

75   territorial defense (Vander Wal and Rodgers 2012, Asensio et al. 2014).

76   The concept of a core area is different from the concept of a territory because the two are based

77   on different assumptions as we intend them: a core area is defined in terms of intensity of use,

78   meanwhile a territory is defined as the area exclusively occupied and defended by a group (Asensio et

79   al. 2014). Core areas can be identified within territories or in non-defended home ranges; however, a

80   core area can be considered a territory if it represents the area of the range that is exclusively occupied

81   and defended against intrusions (Bates 1970, Wartmann et al. 2014). In our study, we identified the

82   core areas as the smallest area of the territory in which a group spent at least 50% of the observation

83   time.

84   On the other hand, groups tend to avoid certain locations, if there is a risk of potentially

85   dangerous intergroup encounters (Wrangham et al. 2007). For example, in the case of Javan gibbons

86   (*Hylobates moloch*), individuals - especially males – select sleeping sites away from the location of

87   encounters (Yu et al., this special issue), and capuchin monkeys (*Cebus capucinus*) tend to reduce the

88   risk of encounters by avoiding shared or peripheral areas of territories or home ranges (Torrez, this

89   special issue).

90   A strategy to reduce the costs associated to territorial defense is the use of signals that allow

91   long-distance communication, reducing the occurrence of physical encounters or fights. Loud calls play

92   an essential role in signaling territory occupancy or defense and can trigger responses affecting the

93   spacing patterns of neighboring groups (Pollock 1986, Cowlishaw 1992). The spatial responses to

94   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

118   least 16 days of observation to reach an accurate estimate of territories size (Pollock 1986, Bonadonna

119   et al. 2017).

120   To communicate at inter and intra group level, indris emit songs in choruses that can vary in

121   size ranging from two individuals – usually the reproductive pair – up to five (Torti et al. 2018). The

122   song is a cost-efficient way to communicate on long distances and one of the main functions is to

123   regulate territorial occupancy besides broadcasting individual cues (Gamba et al. 2016, Torti et al.

124   2017).

125   Previous studies show that advertisement and territorial songs have different characteristics and

126   can be recognized depending on their acoustic structure and the context of emission. Advertisement

127   songs are emitted in the absence of visual contact between groups, they are shorter in duration and the

128   overlap between notes is limited; territorial songs are only emitted when groups are in visual contact on

129   a territorial boundary, they can last five times more than the average advertisement song and

130   individuals' contribution highly overlap (Torti et al. 2013). In this species, intergroup encounters are an

131   infrequent occurrence (on average one encounter every 20 days), restricted to the peripheral areas of

132   the territory (on average within 22 m from the boundaries). In the majority of cases, the encounters are

133   solved with the emission of territorial songs (87% of reported cases) and, rarely, they can involve

134   chasing and physical fights (13% of cases reported) (Bonadonna et al. 2017).

135   This study wants to investigate the relationship between social and spatial dynamics in a pair-

136   living territorial primate, and if if a differential intensity of space use within a territory can be related to

137   intergroup dynamics. Because of the fine regulation of territory exclusivity between neighboring

138   groups and the rare use of songs among primates, the indri is an interesting model to study the

139   implications of space use on intergroup dynamics over time. In this study, we aim to extend previous

140   findings on the spatial behavior of this species (Bonadonna et al. 2017) thus investigating: (i) the

141 stability of the territories across time, (ii) the presence and stability of core areas over time, (iii) the

142 spatial distribution of singing locations and intergroup encounters within the territories (core areas vs.

143 non-core area).

144   We hypothesize that indris would show a pattern of territorial stability similar to those found in

145 other pair-livings territorial primates, and that over time the pattern should reflect the history of spatial

146 dynamics between groups, with a tendency to maintain high territorial stability to reduce the costs

147 associated with spatial mediation between neighboring groups (Wartmann et al. 2014, Bartlett et al.

148 2016, Fernandez-Duque 2016, Van Belle et al. 2018). Therefore, we predict that indri groups might

149 occupy the same area across successive periods with a limited territorial shift.

150   In the case of folivorous species - such as the indri - food resources are constantly available and

151 not patchily distributed (Milton and May 1976), previous studies on indris' diet found that immature

152 foliage (preferred food item) are available all year around (Powzyk and Mowry 2003). In the prediction

153 of site fidelity, a territory should contain the resources needed in the long term, and core areas are

154 assumed to contain important resources for survival. However, ecological needs might not be the only

155 drivers in the pattern of space use and groups may spend more time in certain areas in response to

156 territorial dynamics and the necessity of territory exclusivity (Asensio et al. 2014).

157   Because indris require long-term preferred food resources availability, and they regulate

158 territorial dynamics without an intense patrolling of the boundaries, we expect that indris would have

159 core areas that are not stable in successive years with low values of overlap over time, shifting areas

160 intensely used within territories according to availability of food resources and territory exclusivity.

161   The costs given by the interactions with neighboring groups play a role in the spatial dynamics

162 of a species. In the indri, the overlap between territories is extremely low, the intergroup encounters are

163 at medium risk of aggression (Wrangham 2007, Koch et al. 2016) and are restricted to the peripheries

164   of territories (Bonadonna et al. 2017). Hence, we expect to find higher intensity of use within areas

165   constantly occupied by groups across years, and that peripheral areas might be affected by contentions

166   between neighboring groups.

167   Previous studies suggested that indris' calling has an effective distance that extends up to two

168   kilometers, beyond the range of a single territory (Pollock 1986, Torti et al. 2017), and thus we predict

169   that calling locations would not necessarily reflect a pattern of distribution associated with the core area

170   but they would rather be evenly distributed within a territory, playing a role in mediating the spatial

171   relationship between groups.

172   **Material and Methods**

173   **Study Site and Subjects**

174   The New Protected Area (*Nouvelle Aire Protégée*, NAP) of Maromizaha (18° 56' S, 48° 27' E)

175   is part of the forest corridor Ankeniheny-Zahamena (CAZ). It is located in the Alaotra-Mangoro region,

176   in the district of Moramanga, center-eastern Madagascar. Maromizaha extends for 1880 ha and

177   comprises primary and secondary mid-altitude (800 -1200 m) tropical evergreen rainforest, with an

178   annual rainfall of 1779 mm and an endemism rate of 77% (Randrianarison et al. 2015). This kind of

179   forest is a formation characterized by a single stratum from 20 to 25 m high, above an undergrowth of

180   plentiful shrubs and herbaceous plants (Koechlin 1972). Maromizaha includes an ecotourism area, but

181   the indri groups included in this study are located in the off-limit research area, avoiding exposure to

182   tourists that might affect the behavior of the focal groups. This study includes spatial data collected on

183   three habituated indri groups (1MZ, 2MZ, 3MZ) (Table1).

184   **Table 1. Data set description.** For each group, we provided group size and composition

185   (af/am: adult female and adult male, sam/saf: sub-adult male and female, jf/jm: juvenile female and

186   male; j: juvenile sex unknown) total number of locations recorded for that study period, the number of

187   sampling days and months of data collection.

188

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	

189

190   **Data Collection**

191   We collected data on the three focal groups during four study periods, between 2009 and 2014 (Table

192   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

216 were included in the study. All the field operators followed the same protocol, including researchers

217 and trained research guides that contributed to data collection.

218 **Spatial and Statistical Analysis**

219 All spatial data were analyzed in ArcGIS 9.3 or ArcGIS 10.1 (ESRI 2012). We calculated the

220 linear extension of the territories using Minimum Convex Polygon (MCP) 100% since the data set is

221 robust enough to obtain estimates of the territories with an accuracy higher than 90% (see Bonadonna

222 et al. 2017 for methodological details). All the statistical tests were performed in IBM SPSS 22. The

223 datasets analyzed during the current study are available from the corresponding author on reasonable

224 request.

225 *Territory Stability*

226 We investigated the degree of stability of the territories across four study periods using three

227 different parameters: the variability in size of a territory between two consecutive study periods, the

228 extent of territory persistently occupied by a group across the years (overall stable area), and the shift

229 of the geometric centroids of a territory between consecutive study periods. We reported the size of

230 territories in hectares (ha) for each study period, and we calculated the size variability as the absolute

231 value of change in percentage of territory size between two consecutive study periods. To describe the

232 extent of variability of the territories size across years, we calculated the coefficient of variation (CV)

233 for each group.

234 To obtain the persistent area occupied by a group over time, we followed the methodology

235 described in previous studies on territories and home range stability in primates (Janmaat et al. 2009,

236 Asensio et al. 2012, Bartlett et al. 2016). We overlapped all the annual MCPs of a group first, and then

237 calculated the Minta Index (1992):

238
$$\frac{\cap_{i=1}^{n} a^{i}}{\sqrt[n]{\Pi_{i=1}^{n} a^{i}}}$$

239   Where $\cap_{i=1}^{n} a^{i}$ is the overall intersection of "n" areas ("n" representing the number of annual

240   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

241   territory extensions obtained for each group. The Index can range between 0% (no overlap) and 100%

242   (complete overlap) among areas. Values between 0-33% are classified as low overlap, 34-66% as

243   moderate overlap, and 67-100% as high overlap (Kernohan et al. 2001). We also reported the

244   percentage of overlap of annual MCP with the overall stable area for each group (and respective CV)

245   and calculated the overlap of territories between two study periods, in terms of percentage of territories

246   maintained in the following year.

247   Finally, to quantify the centroid shifts, we computed X and Y coordinates of the geometric

248   centers of annual MCPs (100%) using the "Spatial Analyst" tool in ArcGis 9.3 (Hooge and Eichenlaub

249   2000). We then calculated the linear distance (m) between centroids observed in two consecutive

250   periods.

251   *Core area designation and stability*

252   In our dataset, the time spent by a group in each recorded GPS waypoint may vary, depending

253   on how long a group remained in a stationary area. Hence, in our dataset the number of waypoints itself

254   does not reflect the intensity of use of an area. To indicate the differential intensity of use within each

255   territory, we created a grid with hexagonal cells of .50 ha each, by using the ArcGis extension Patch

256   Analyst (Rempel and Kaufmann 2003; Asensio et al. 2012). By summing the minutes spent at each

257   waypoint included in a cell, considering only cell grids in which the stationary area centroids are

258   contained, we obtained the cumulative time spent at each hexagon by a group.

259   To evaluate a differential intensity of use throughout the territory, we identified four classes of

260   intensity of use of each cell based on the minutes spent in each hexagon by using ArcGis to classify

261   them. To standardize the different times among groups, we set between 0 and 100% the minimum and

262   maximum time spent for each group in a cell and set break values at interval of 25%. We obtained a

263   map showing a gradient intensity of use throughout the territory, Electronic Supplementary Material 1

264   (ESM1) reports the territory size calculated with the method of the hexagonal grid for comparison

265   purposes.

266   Afterwards, we ordered the cells according to their time values, and we manually identified the

267   smallest number of cells that made up to 50% of the observation time. This allowed us to identify the

268   smallest area of the territory in which a group spent at least 50% of the time, which represents the core

269   area. We excluded a potential correlation between the percentage of territory representing the core area

270   and absolute territory size by running a Pearson's correlation (Pearson's correlation: 0.1, P=0.656,

271   N=12). Because the sampling span is not homogeneous across study periods, we tested with a

272   Spearman's Rho an eventual correlation between the sampling effort as number of months per study

273   period and the size of the core areas, however we did not find a significant correlation (Spearman's

274   Rho: rs = 0.4, P=0.227, N=12).

275   To estimate the stability of the identified core areas across study periods, we overlapped yearly

276   core areas obtaining the regions consistently maintained as core area across time (overall stable core

277   area) and quantified the parameters of size variability between years and the Minta Index, both

278   calculated as previously described for the territory stability. We reported the extent of core area shared

279   between two consecutive periods for each group, calculated as percentage of core area maintained

280   from the previous year; we obtained the proportion of core area included within the territory in two

281   consecutive years by calculating the percentage of core area included in the MCP of the consecutive

282   study period. Finally, we reported the percentage of core area included in the overall stable area of

283   territories.

284   *Spatial distribution of singing locations and intergroup encounters*

285   We recorded a total of 191 singing locations for the three groups during the entire study: 77, 64,

286   and 50 for the groups 1MZ, 2MZ, and 3MZ, respectively. We plotted the singing locations recorded

287   during a study period on the respective annual core area for each of the three indri groups, then we used

288   the ArcGis tool "point count" to obtain the number of singing locations inside and outside the core area

289   for each territory. We then compared the cumulative frequencies of singing location inside and outside

290   the core areas for each group. We performed a Chi-squared test of goodness-of-fit ($\alpha \leq .05$) to compare

291   the frequency of singing locations between core and non-core areas; we defined expected values,

292   considering the null hypothesis of an even spatial distribution of singing locations, given the fact that

293   the groups spent half of the observation time inside or outside the core areas, according to our

294   definition.

295   We recorded a total of twelve intergroup encounters over the entire study period, four for each

296   group, and we took note if encounters were solved through the emission of territorial songs or if they

297   involved physical fights. We plotted the encounters in the territories, and we reported the percentage

298   located in the core areas; we also counted how many of the encounters were located in the overall

299   stable area of territories. To account for movements of the groups during intergroup encounters, we

300   applied a 20 m buffer (10 m radius) to each encounter point.

301   **Ethical Note**

302   We conducted this study on a wild population of the Critically Endangered (IUCN 2014)

303   species *Indri indri* in the New Protected Area (NAP) of Maromizaha (Madagascar), managed by the

304 GERP (Group d'Etude et de Recherche sur les Primates du Madagascar). During observations, we

305 followed the groups at a distance of 10–50m, avoiding any unnecessary disturbance. All the groups

306 studied were habituated to human presence since early 2009. The groups inhabit an area of primary

307 forest accessible only when a research permit is granted thus, none of the groups has been subjected to

308 eco-tourism. None of the field operators got in physical contact with the animals. The study followed

309 the legal requirements of Madagascar: the "Ministère de l'Environnement et des Forêts" (MEF) of

310 Madagascar reviewed and approved the research methods, and issued the research permits for the field

311 activity and data collection in Maromizaha (N° 243/ 09/ MEF/ SG/ DGF/ DCB.SAP/ SLRSE, N° 118/

312 10/ MEF/ SG/ DGF/ DCB.SAP/ SCBSE; N° 293/ 10/ MEF/ SG/ DGF/ DCB.SAP/ SCB, N° 274/ 11/

313 MEF/ SG/ DGF/ DCB.SAP/ SCB, N°245/12/MEF/SG/DGF/DCB.SAP/SCB,

314 N°066/14/MEF/SG/DGF/DCB.SAP/SCB; N°066/14/MEF/SG/DGF/DCB.SAP/SCB).

315 **Results**

316   **Territory Stability**

317   The map showing the overlapping annual MCPs indicates that the three groups tended to have

318 stable territories across the study period (2009 – 2014) (Fig. 1A). The results are consistent across all

319 the three parameters considered: size variability, intra-group territory overlap, and centroid shift, even

320 if we observed some degree of flexibility among the groups' territories (Table 2 and Table 3).

321   *Size variability*

322 We found an overall mean territory size of 12.7 ± 2.8 ha (N=12), ranging between 9.2 and 17.5 ha

323 (with the method of the grid we obtained an overall average territory size of 16.0 ± 2.5 ha (N=12),

324 ESM1). The overall mean difference in territory size between two consecutive study periods is 10.6 ±

325 5.5 % (N=9), ranging between 13-22% for group 1MZ, 4-7% for group 2MZ, and 8-12% for group

326 3MZ. Group 1MZ showed the greatest increase in territory size over time , group 2MZ had the smallest

327 and most stable territory across years , and group 3MZ was intermediate both in terms of territory size

328 and stability over time compared to other two groups (Table 2). The CVs show a comparable

329 variability in territory size across years among groups (Table 2).

330 *Intra-group territory overlap*

331 According to the Minta Index, we found that the groups 1MZ and 2MZ show high overlap of

332 their territories across time, and group 3MZ is at the upper limit of medium overlap (Table 3). The

333 overall mean percentage overlap between the MCP of a given study period and the overall stable area

334 was 63.9 ± 14.0 % (N=12), ranging between 59.2% (group 3MZ) and 96.3% (group 1MZ). Although

335 group 1MZ presents the highest value of overall overlap of its territory across time, it is also the group

336 with the highest CV (Table 2) indicating higher flexibility in annual territory overlap with the overall

337 stable area. Except for the group 3MZ, the degree of territory overlap between consecutive study

338 periods increased over time (Fig. 2A).

339 *Centroid shift*

340 The centroids showed little shift over time with an overall mean of 32m $\pm$24 (N=12), ranging

341 between 2 m (group 1MZ) and 82 m (group 3MZ). The average shift of centroid between two

342 consecutive periods was 14 ± 11 m (range: 2 - 22 m) for group 1MZ, 32 ± 19 m (range: $15 - 53$ m) for

343 group 2MZ, and 50 ± 28 m (range $34 - 82$ m) for group 3MZ (N=3 for each group). We found the

344 greatest shift of centroids for the group 3MZ between 2010 and 2011, which reflects the lowest values

345 of inter-annual territory overlap found for this group (Fig. 2A). During the same interval of time, we

346 observed a 53 m shift of centroid, the second largest, for the adjacent territory occupied by the group

347 2MZ (Fig. 1A).

348

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.
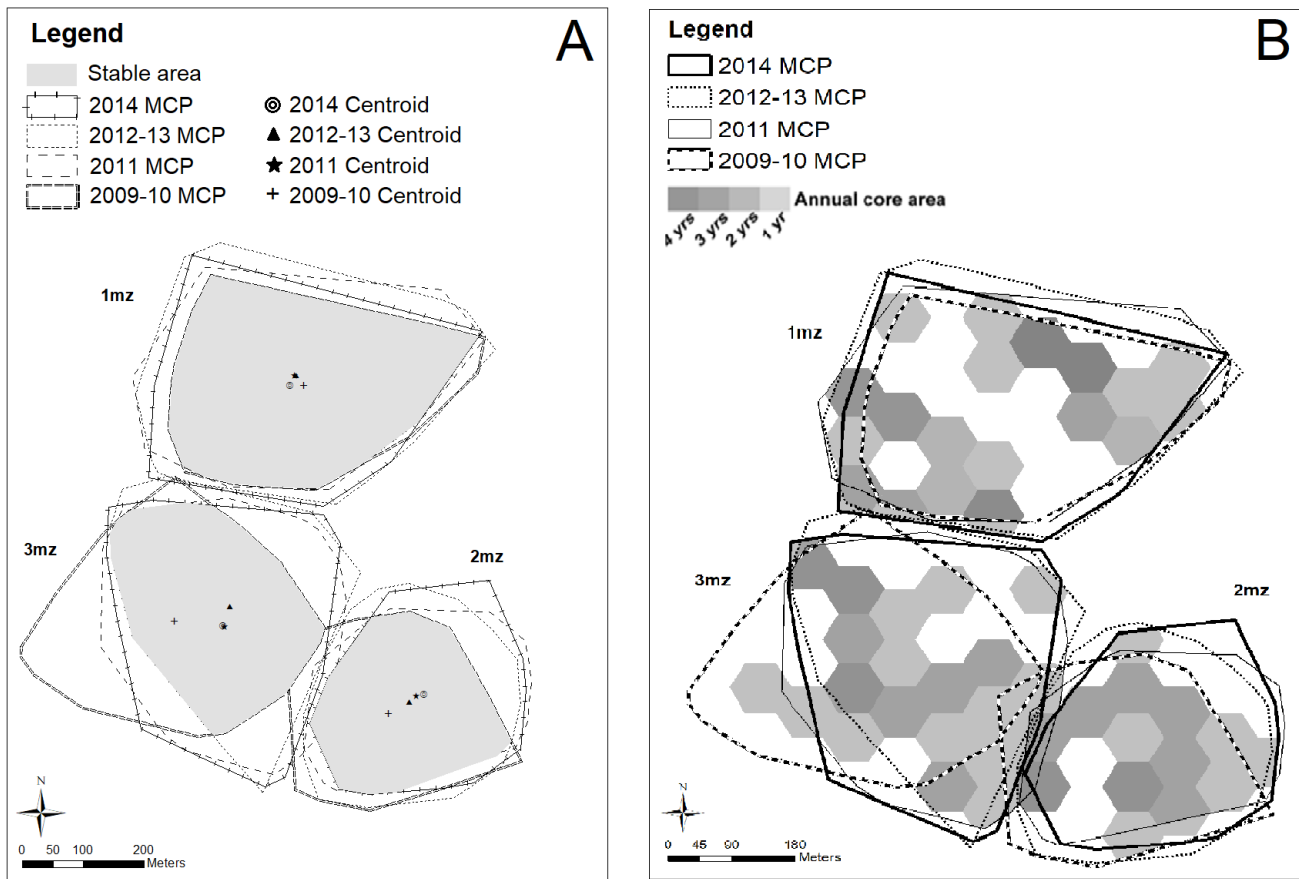
355

356 **Fig. 2. Territory and core area overlap for the indri groups 1MZ, 2MZ, 3MZ over four study**

357 **periods (2009-2014) in the Maromizaha forest, Madagascar.** Lines indicate the inter-annual

358 variation for each group. The star (*) indicates a study period comprising two different years (e.g.

359 2010* comprises both 2009 and 2010). A. Intragroup territories overlap between study periods (%). B.

360 Intragroup core area overlap between study periods (%). C. Extent of core area included in the territory

361 of the consecutive study period (%). D. Extent of core area included in the overall stable area (%). In

362 A, B, and C overlaps are expressed as percentage in relation to the total extension of the consecutive

363 study period. In D. overlap is expressed as percentage in relation to the core area total extension, within

364 the same study period.

365
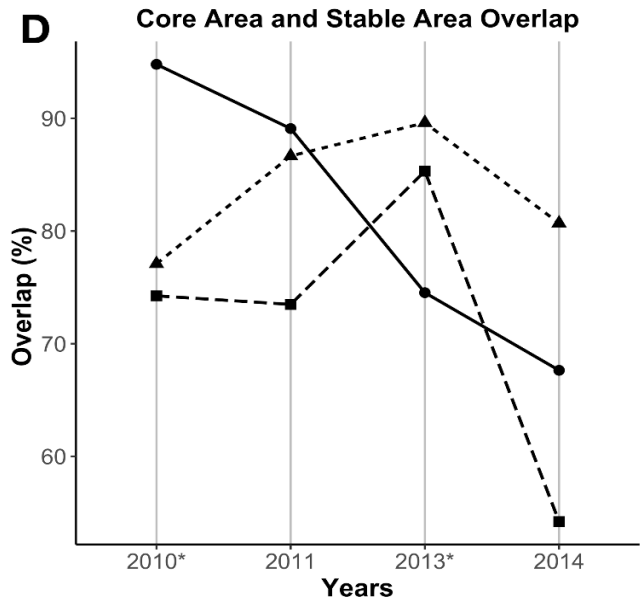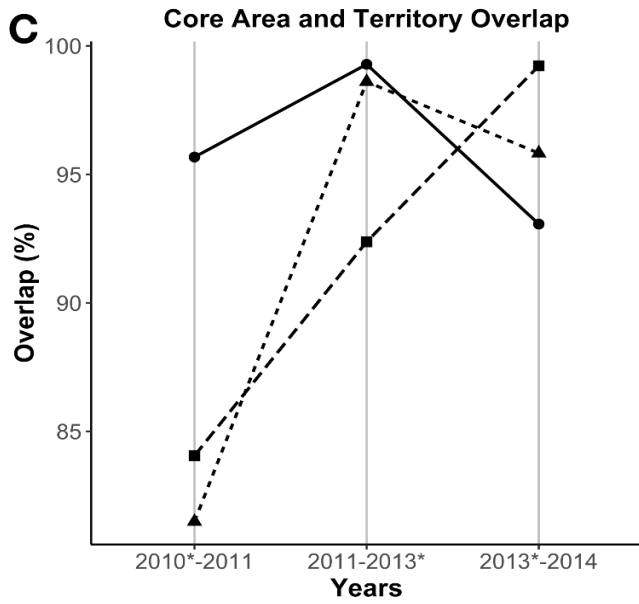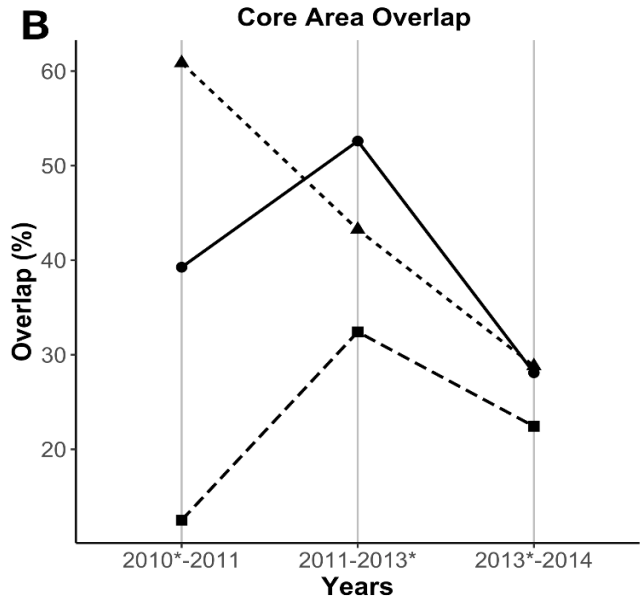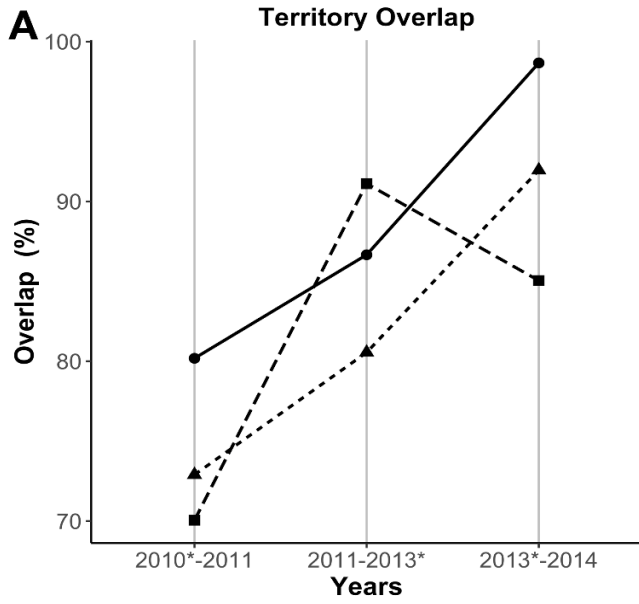
366 **Table 2. Territory and core area size and stable area.** Territory and core area size for each indri

367 group in each sampling period and the respective mean, standard deviation (SD), and coefficent of

368 variation (CV). The table includes the area constantly occupied by a group across sampling periods

369 (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

370

371

372 **Table 3. Terriotry and Core Area Overlap with Respective Overall Stable Area and Minta**

373 **Indices.** Percentage of overlap between the Minimum Convex Polygon (MCP) of a sampling period

374 and overall stable territory; percentage of overlap between the core area of a sampling period and the

375 overall stable core area. We reported mean, standard deviation (SD), and coefficient of variation (CV)

376 for each indri group. Minta Indices represent the degree of overlap for each group (high 67-100%,

377 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

378

379

380 **Intensity of Use and Core Area**

381   We found that areas at higher intensity of use can have a scattered distribution through a

382 group's range and can be located in the center as well as in more peripheral areas of a territory. The

383 same is true for the areas less intensely used by a group in a given year (Fig .3).

384   Quantifying the size of the core area for all the groups for all study periods, we determined that

385 the groups spent 50% of their time in a mean area of 3.4 ± 0.8 ha (N=12), with the core area

386 representing $26.7 \pm 4.7\%$ (N=12) of the territories (ESM2). Considering each group separately across

387 the four study periods, we found that the core area represents $24.0 \pm 4.4\%$ (N=4) of the territory for the

388 group 1MZ, $29.0 \pm 5.1\%$ (N=4) for the group 2MZ, and $27.1 \pm 4.1\%$ (N=4) for the group 3MZ. Core

389 areas of neighboring groups never overlapped during a study period, although they could be adjacent to

390 each other (Fig. 4).

391   We found considerable variation in core area size and location across time. Core area sizes

392 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

393 group 3MZ (Table 2). We found a greater change of core area size between study periods compared to

394 the variability found for territory size, with an overall mean change of 22.2 ± 18.7 % in size between

395 consecutive study periods (N=9). The high CVs indicate that the core area size of a group can greatly

396 vary from a year to another (Table 2).

397

398   **Fig 3. Intensity of use**. The territories of three indri neighboring groups in four study periods

399   between 2009 and 2014 are shown. The outlines represent the Minimum Convex Polygons (MCP).

400   Different shades of gray represent the intensity of use in terms of time spent in a cell by a group as

401   percentage of the total time of observation. The lined pattern indicates overlapping cells between

402   groups.
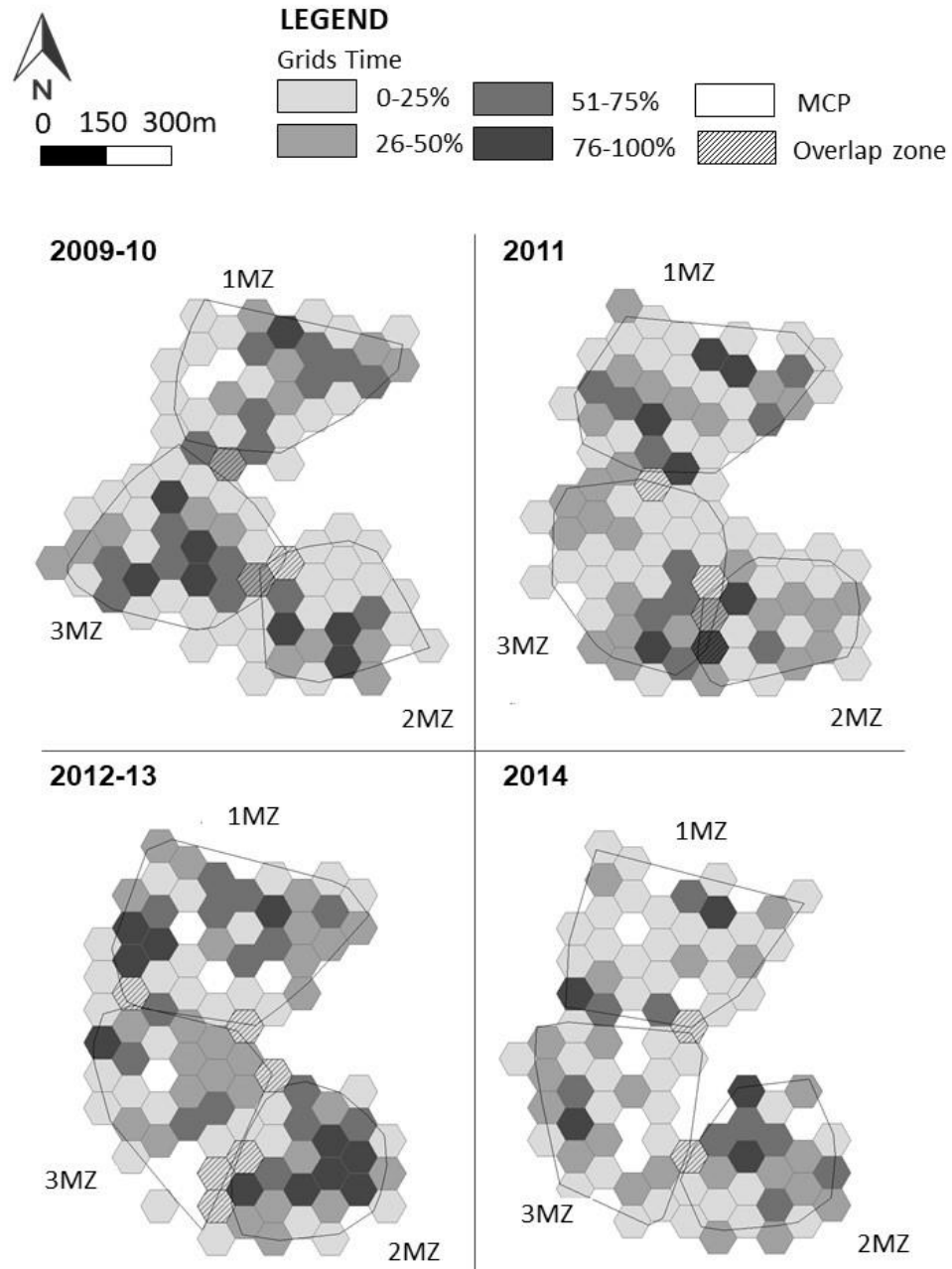
403

404   **Fig. 4. Core Area, spatial distribution of singing locations and intergroup encounters of**

405   **three indri neighboring groups in Maromizaha, Madagascar, during four study periods.**

406   Spatial distribution of core area (gray cells), singing location (stars), and intergroup encounters (circles)

407   in each indri territory (MCP) during four study periods between 2009 and 2014 (each box represents a

408   different period). The encounters include a 10 m radius buffering area. The black dot marks the only

409   intergroup encounter that involved a physical fight besides the emission of territorial songs (2011).

410

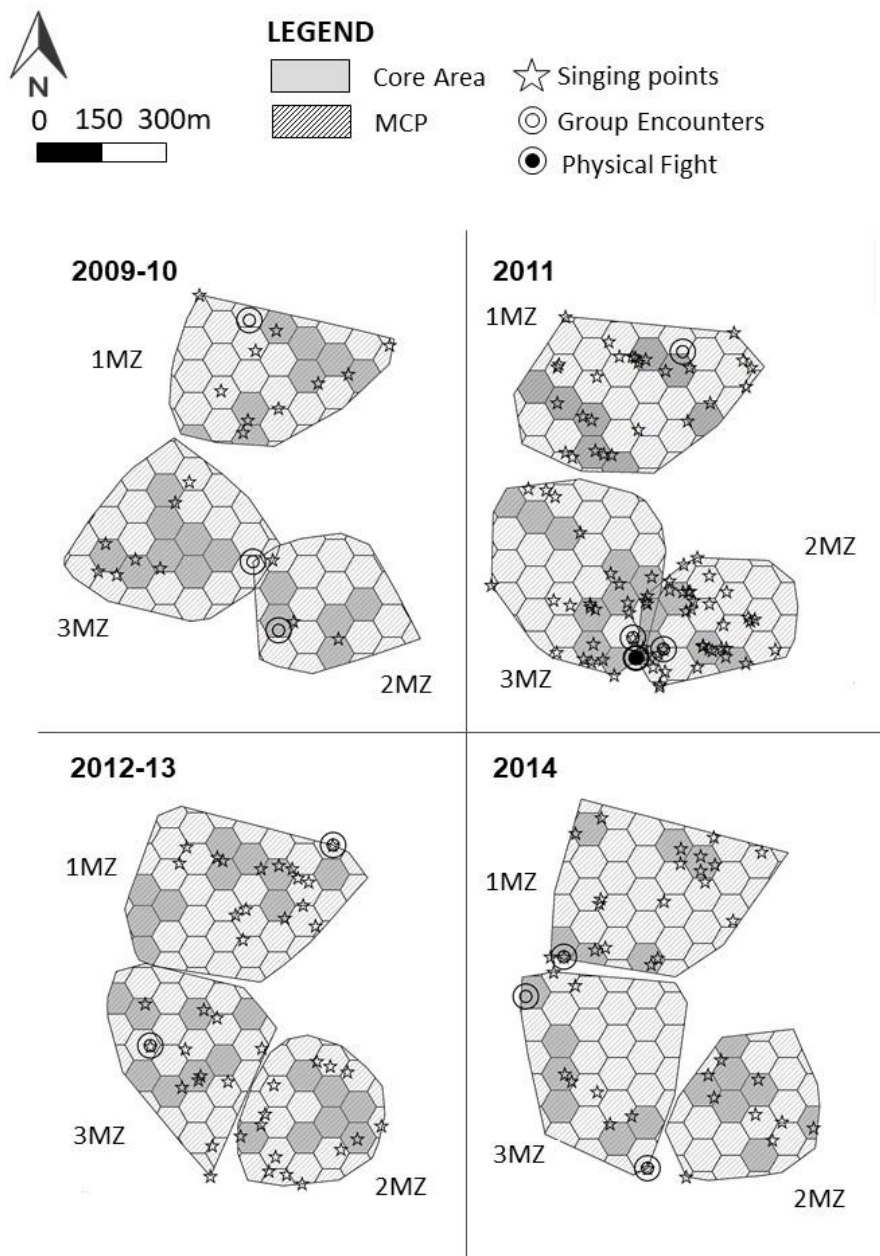411   All three indri groups exhibited low overlap of core areas across years (Table 3). The only

412   group presenting core area overlap throughout the four study period was 1MZ; even if they occupy a

413   smaller territory than the group 1MZ, neither group 2MZ nor 3MZ had an overall stable core area

414   (Table 2 and 3). When considering the overlap of core areas between two consecutive study periods,

415   we found a certain degree of intersection for all the groups (ESM3). Group 2MZ showed the highest

416   percentage of core area overlap between two consecutive periods (61%), although decreasing over

417   time. Meanwhile, the groups 1MZ and 3MZ showed a similar pattern of overlap between two years

418   over time, with group 3MZ presenting the lowest values, ranging between 13% and 32% (Fig. 2B).

419   Considering the distribution of core areas within a territory, we found an overall mean of 93.3% ±6.5%

420   (N=9) of core areas still included as part of the territory in the following year. Group 1MZ showed an

421   overlap higher than 90% in all years, the other two indri groups presented a general increasing trend

422   with the last period presenting overlap values over 95% (Fig. 2C). Across the study period, we found

423   that on average 78.9 ± 11.2 % (N=12) of core areas are located in the overall stable area, ranging

424   between 95.8% (group 1MZ) and 54.2% (group 3MZ) (Fig. 2D).

425   **Spatial distribution of singing locations and intergroup encounters.**

426   Fig 4 shows the spatial distribution of the singing locations and intergroup encounters within

427   the territories of the focal groups in a given study period. On a total of 191 singing locations recorded,

428   98 were inside the core areas. Considering the cumulative number of singing locations for each group,

429   we obtained a mean proportion of 55.9% ± 5.2 (N=3) of songs emitted from the core areas. We did not

430   find a significant difference in the frequency of singing locations distribution between core and non-

431   core areas for any of the three groups: for group 1MZ, 37 locations (48.1%) were in the core area (χ^2

432   (1, n =77) = .117, P=.732); for group 2MZ, 32 locations (50.0%) were in the core area (χ^2 (1, n =64) =

433   .000, P=1); for group 3MZ we found 29 locations (58.0%) in the core area (χ^2 (1, n =50) = 1.280,

434   P=.258).

435   We found that on a total of 12 intergroup encounters, 60% were located in the core areas. All

436   the encounters were solved through the emission of territorial songs except for one encounter between

437   the groups 2MZ and 3MZ in 2011, when the two groups were involved in a physical fight. It is worthy

438   to note that three of the four encounters recorded in 2011 involved the groups 2MZ and 3MZ,

439   following a shift of the territory of group 3MZ toward the East side that resulted in an overlap between

440   the two groups (Fig 4). Figure 4 shows, that in the following study periods, the vocal activity and

441   intergroup encounters decreased compared to 2011 and the territories of the group 2MZ and 3MZ did

442   not overlap. It is interesting to note that group 3MZ was in the numeric majority; in 2011 group 3MZ

443   was composed of four individuals including three singers and a two-year-old non-singing juvenile,

444   meanwhile the groups 2MZ was composed of the reproductive pair only after losing their last infant in

445   2010 (Table 1). Also, in 2011 the female of group 3MZ (Mena) was involved in the Extra Pair

446   Copulation with the reproductive male of the group neighboring on the West side.

447   **Discussion**

448   Our study provides information about the stability of territories and space use over time in the

449   indri. Territories were stable in terms of both size and location over four study periods. Our study

450   confirmed the presence of core areas shifting over time, but remaining part of the territory in successive

451   years, and tending to be concentrated in the stable area of a territory. In particular, we found that there

452   are areas intensively used over a multi-annual span, and others that have never been included in a core

453   area during the entire study period. Our results indicate that none of the three indri groups called more

454   frequently from core areas than the rest of the territory, and that intergroup encounters - although rare -

455   are more frequent in peripheral areas that are also intensively used by a group.

456 *Territory stability*

457   The indri groups showed a degree of site fidelity comparable with other pair-living primates

458 (White-handed gibbons, *Hylobates lar* (Bartlett et al. 2016); Kloss' gibbons, *Hylobates klossii* (Tenaza

459 1975); titi monkeys, *Callicebus spp* (Robinson et al. 1987); fat-tailed dwarf lemurs, *Cheirogaleus*

460 *medius* (Fietz 2003); owl monkeys, *Aotus azarae* (Wartmann et al. 2014)). This pattern of high stability

461 implies that a territory contains all the resources needed to support a group over the long term (Vander

462 Wal and Rodgers 2012, Bartlett 2015). In a mainly folivorous species that occupies small territories,

463 such as the indri, the pattern of food distribution and its availability in space and time does not seem to

464 represent the principal variable in determining the pattern of space use.

465   According to our results, high stability can be explained as a strategy that limits the costs of

466 spatial competition between groups to keep the exclusive use of the territory and, in a pair-living

467 system, to ensure the exclusive access to the partner. Once territorial boundaries are set, opportunities

468 to shift territories without risking conflicts with neighboring groups are rare. The territorial dynamics

469 and sequential shift observed between the groups 2MZ and 3MZ (including the only case of physical

470 fight reported in our study) suggest that territorial advertisement and defense are related to the

471 necessity of territory exclusivity, which is considered a prerequisite in maintaining a pair-living

472 sexually monogamous mating system (Reichard and Boesch 2003). The group with weaker stability

473 (3MZ) was the same involved in the only extra pair copulation (EPC) observed in this species

474 (Bonadonna et al. 2014), suggesting that less territorial stability may coincide with social and

475 reproductive inter-group dynamics.

476 *Core area*

477   We found evidence that all the groups invested half of their time spent in stationary activities

478 in less than a third of their territory that we identified as the core area. The intensive use of an area

479   within a territory is a common pattern among primates (e.g. chimpanzee (*Pan troglodytes*: Herbinger et

480   al. 2001), howler monkeys (*Alouatta guariba clamitans*, *Alouatta caraya* : Agostini et al. 2010), owl

481   monkeys (Aotus azarae: Wartmann et al. 2014), and gibbons (Hylobates lar, Asensio et al. 2014)); we

482   found that for the indri, the portion of territory occupied by a core area is independent of absolute

483   territory size, suggesting a link between size variability of the core areas and the respective territory

484   extension.

485   We found that core areas shift across years but tend to be included in the territory of the

486   successive year, and across years they cover the whole territory. Similar results have been found in

487   multi annual studies on white-handed gibbons (Hylobates lar) (Bartlett et al. 2016) and on spider

488   monkeys (Ateles geoffroy) (Asensio 2011), although both species are highly frugivorous and a shift of

489   the core areas has been explained with changes in preferred food availability over time (Asensio et al.

490   2014), the results are in agreement with the importance for territorial species to occupy an area that

491   include future core areas. On the other hand, a long-term study on another population of spider

492   monkeys found that core areas were more stable than home range, probably due to a high fidelity to

493   locations of high-quality habitat (Ramos-Fernandez et al. 2013), suggesting that there can be a patter

494   variation at intraspecific level due to the locations of such habitat (Ramos-Fernandez et al. 2013).

495   Because of a similar pattern in home range and core area stability between species with

496   different diets, and a different pattern between populations of the same species, we can infer that

497   resources location are surely important in defining space use dynamics over time, but the role of

498   territorial defense and control to mate access in pair-living species is also a contributing factor, as mate

499   location is less predictable than the location of food resources.

500   Although indris base more than 70% of their diet on young leaves and 16% on fruits (Powzyk

501   and Mowry 2003), we do not exclude that other factors may influence the differential intensity of space

502   use in this species. These factors may be ecological, such as the regeneration of young leaves, or the

503   distribution in space and time of preferred resources, or geographic features of territories (i.e., the

504   presence of rivers and falls or the topography of the territories). Our current data does not allow us to

505   draw conclusions on this point and this hypothesis requires further investigation.

506   *Group dynamics and intergroup encounters*

507   Different studies found evidence that overlapping zones between territories, although limited in

508   size and occurrence compared to non-territorial species, tend to be underused especially when there is

509   the risk to incur in potentially dangerous fights with neighboring groups (Wrangham et al. 2007, Torrez

510   this issue). In agreement with previous findings, the overlap between territories is almost absent in

511   indris (Bonadonna et al. 2017); given the fact that indri groups do not share areas of their territories, it

512   is not surprising that in this species intergroup encounters are rare, although they can occur.

513   Most of the encounters were located in heavily used areas located at the periphery of territories,

514   which suggests that spending time at the border increases the probability to engage in an intergroup

515   encounter, despite the limited or absent overlap between territories. On the other hand, groups may

516   spend more time in areas where an intergroup encounter took place to defend a disputed area of the

517   territory. Furthermore, we found that even if core areas were located in the peripheral area of a

518   territory, they are more concentrated in the overall stable area occupied by a group, suggesting the

519   tendency to concentrate activities in areas less affected by shifts over time potentially contended

520   between groups.

521   Through the emission of songs, indris maintain an exclusive use of the territory, limiting the

522   necessity of physical confrontation. This strategy of territorial defense and exclusivity can also

523   reinforce an active mate guarding strategy: having exclusive territories and minimizing the risk of

524   physical encounters can be a strategy to monopolize access to the female (Reichard and Boesch 2003).

525 During intergroup encounters, males of territorial species can discourage neighboring males

526 attempting to mate with the resident female (Koch et al. 2000), while at the same time displaying their

527 ability to defend a territory (Kempenaers and Dhondt, 1993).

528   A comparison between the rate of intergroup encounters and the mating system in indris and

529 gibbons provides a good example. Intergroup encounters in indris are rare. Previous studies reported

530 only one observation of Extra pair Copulation (Bonadonna et al. 2013) and genetic monogamy seems

531 to be the norm in this species (Bonadonna et al. 2019). On the other end, studies on gibbons showed

532 that they present a high rate of intergroup encounters, and pair-living females are sexually promiscuous

533 with higher rates of extrapair copulation compared to the indris (Reichard and Barelli 2008, Barelli

534 2013), although intergroup interactions in white handed gibbons are not exclusively agonistic (Bartlett

535 2003).

536 *Singing locations*

537   We found that the indri's advertisement songs are equally distributed inside and outside the core

538 areas, relative to the time spent by a group in those areas. The fact that core areas shift over time can

539 justify the strategy to advertise groups' presence throughout their territories rather than concentrate the

540 advertisement in areas more intensely used in a relatively short term. Indris groups emit on average 2.2

541 advertisement songs per day (Torti et al. 2013) and the signal can reach far beyond the territory extent,

542 eliminating the necessity to broadcast the signal from certain locations so that it would reach receivers

543 located outside the territory.

544   Our results are in line with the proposed role of advertisement songs in indri in maintaining

545 territory occupancy (Pollock 1986, Geismann and Mutcschler 2006), reducing the necessity of

546 incurring in more costly intergroup confrontations. This description fits with the model of regular

547 advertisement of occupation, which predicts the spread spatial distribution of loud calls within a

548   territory when they have the function of signaling territory occupancy (da Cunhna and Byrne 2006).

549   The same model has been suggested for howler monkeys (*Alouatta pigra*, Van Belle et al. 2013), while

550   in kloss gibbons (*Hylobates klosii*) most of the post-dawn singing locations are placed in what the

551   authors call "most used area" (Whitten 1982). On the other hand, the spatial distribution of territorial

552   songs (emitted exclusively during intergroup encounters) is limited to the boundaries, fitting with the

553   model of territorial boundary marking and defense (da Cunhna and Byrne 2006) and in accordance

554   with the proximate cause of territorial songs previously proposed for this species (Torti et al. 2013). In

555   conclusion, we believe that given the pronounced territoriality of this species, and the efficient spacing

556   regulation between neighboring groups, the pattern of space use in indris is influenced by intergroup

557   dynamics and that vocal communication plays an important role.

558   It is recognized that the maintenance of stable and exclusive territories, as we found for indri, is

559   a prerequisite for the evolution and maintenance of a pair-living monogamous mating system (Reichard

560   2003). However, not all pair-living primates are territorial and vice-versa. A system in which pair-

561   living and territoriality are strictly bound may require the evolution of strategies to regulate

562   communication and relationship at the inter-unit level, because units compete and are not independent

563   of each other (Fuentes 2000, Tsai 2002, Bartlett 2003, Furuichi this special issue).

564   From their studies on white handed gibbons, Bartlett and colleagues (2016) suggested that

565   social factors can also drive space use besides ecological factors, and that to better understand the

566   behavioral ecology of a species, social units should not be considered independently but as part of a

567   network. We found a similar pattern in the indri, a species with a different feeding ecology when

568   compared to gibbons, but with many similarities in their social organization and vocal communication.

569   However, the relevance of the link between the social organization and mating system with external

570   and ecological factors is an idea that has been suggested decades ago (Tsai 2002, Bartlett 2003).

571   Further studies on the spatial and temporal distribution of preferred food resources are needed to have a

572   more complete understanding of the role of ecological variables in the differential intensity of use

573   within an indri territory over time.

582   **Conflict of interests**

583   The authors declare that they have no conflict of interest.

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