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

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(Article begins on next page)

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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. --Manuscript Draft--

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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	

	<p>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.</p>
<p>Suggested Reviewers:</p>	<p>Lydia Light llight1@uncc.edu Expert in behavioral ecology and spatial dynamics of territorial monogamous primates</p> <hr/> <p>Thad Bartlett thad.bartlett@utsa.edu Expert of gibbons behavioral ecology, including long term territory stability.</p> <hr/> <p>Adriano Lameira arel@st-andrews.ac.uk Expert in animal vocal communication</p>

Line 71 - replace comma with semicolon, place comma after "indeed," and change 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.

2009-10

Legend

● Stationary area

□ MCP

Grid Home range

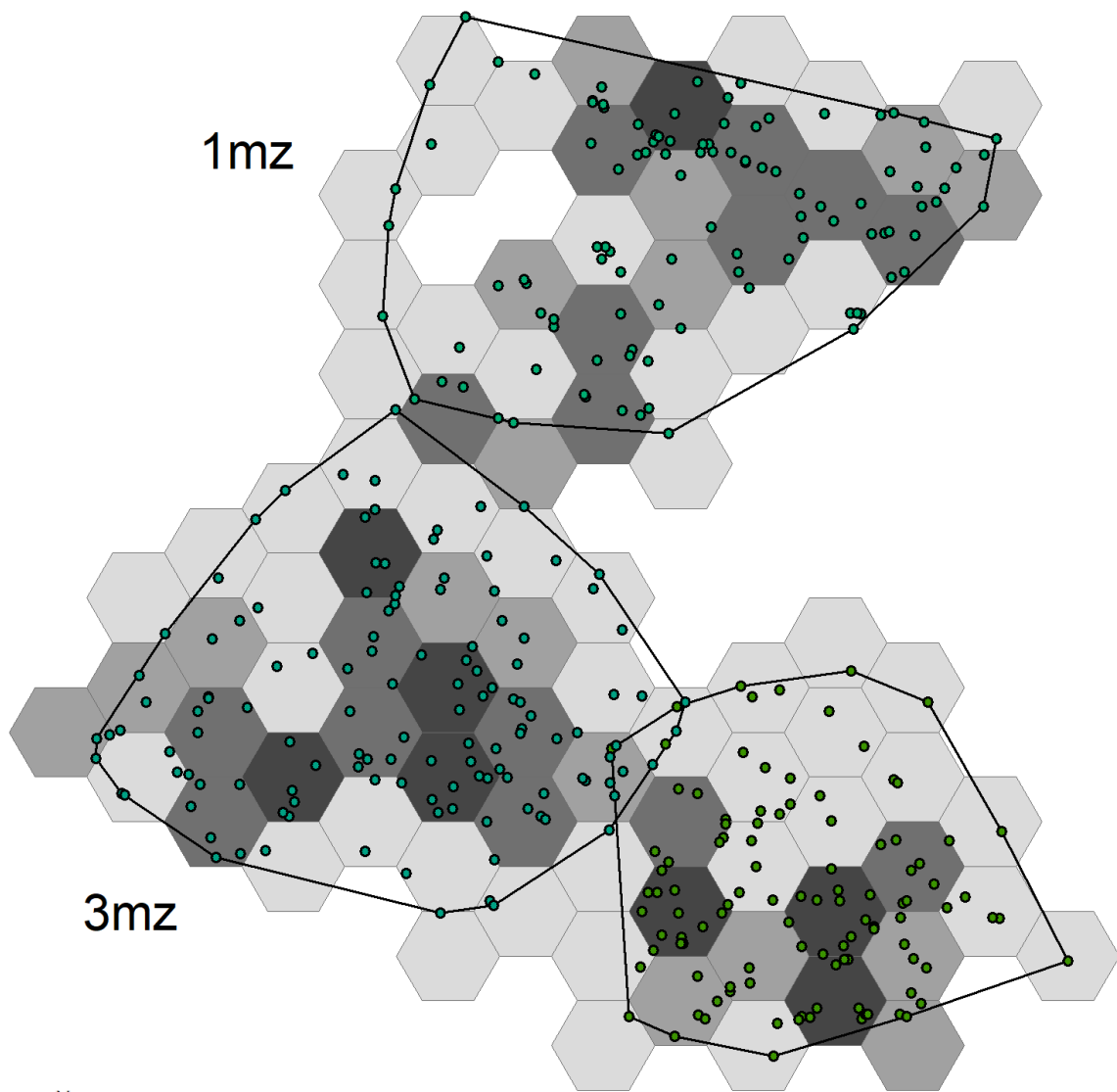
DurataGP_1

0 - 25%

26 - 50%

51 - 75%

76 - 100%



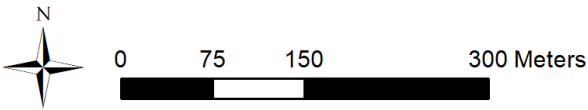
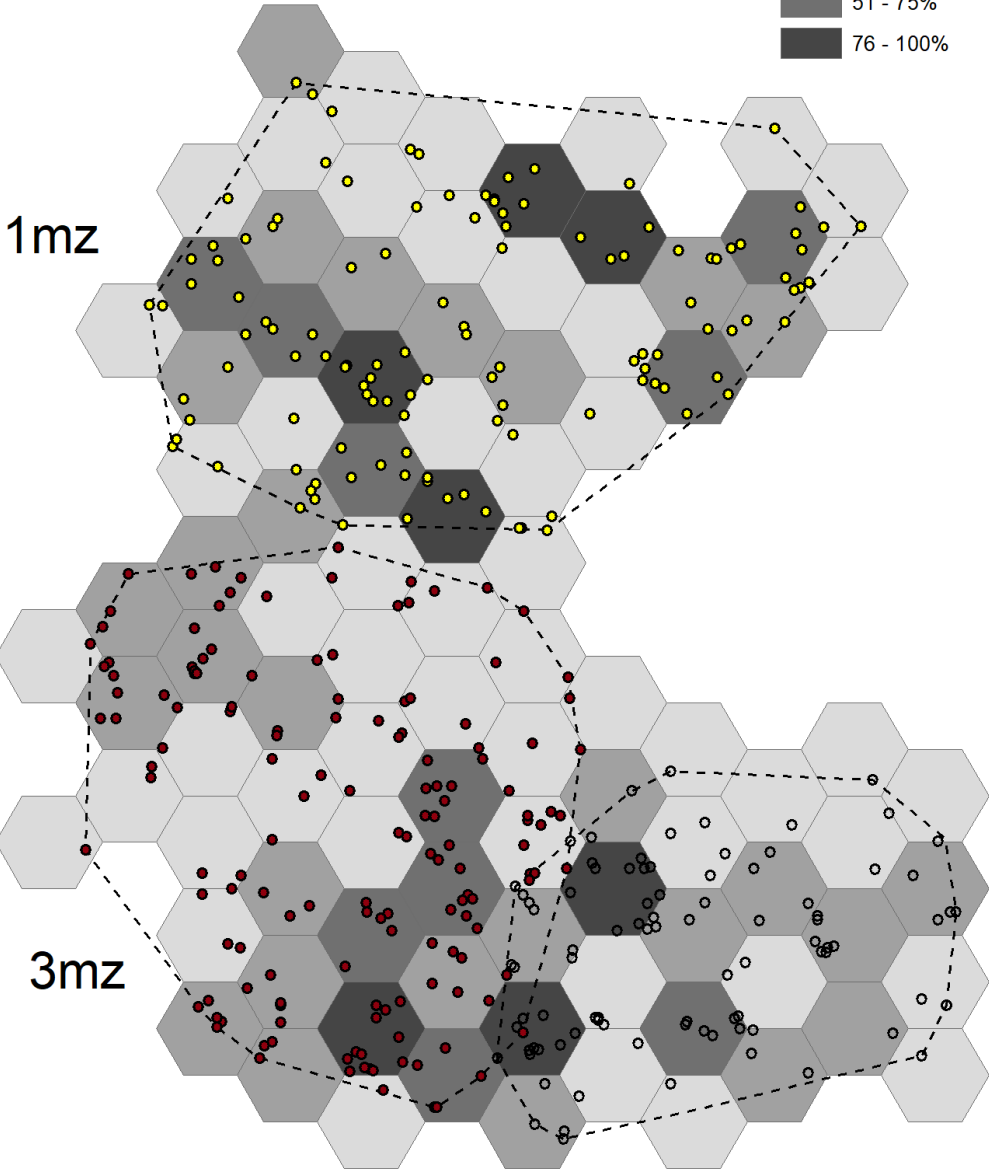
0 75 150 300 Meters

2mz

2011

Legend

- Stationary area
- ⋮ MCP
- Grids Home Range**
- Time**
- 0 - 25%
- 26 - 50%
- 51 - 75%
- 76 - 100%



2mz

2012-13

Legend

● Stationary area

□ MPC

Grid Home Range

DurataGP_1

0 - 25%

26 - 50%

51 - 75%

76 - 100%

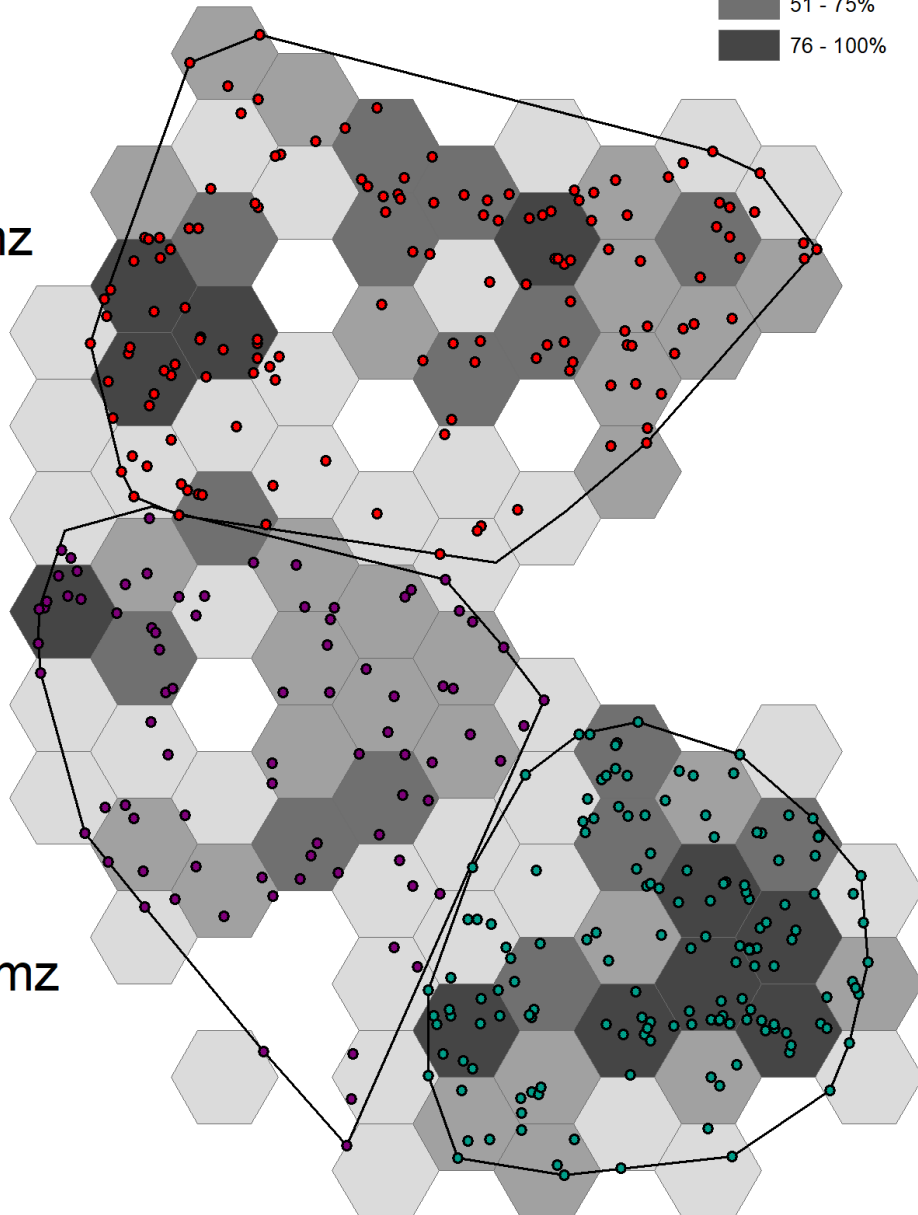
1mz

3mz

2mz



0 75 150 300 Meters



2014

Legend

• Stationary area

--- MCP

Grid Home Range

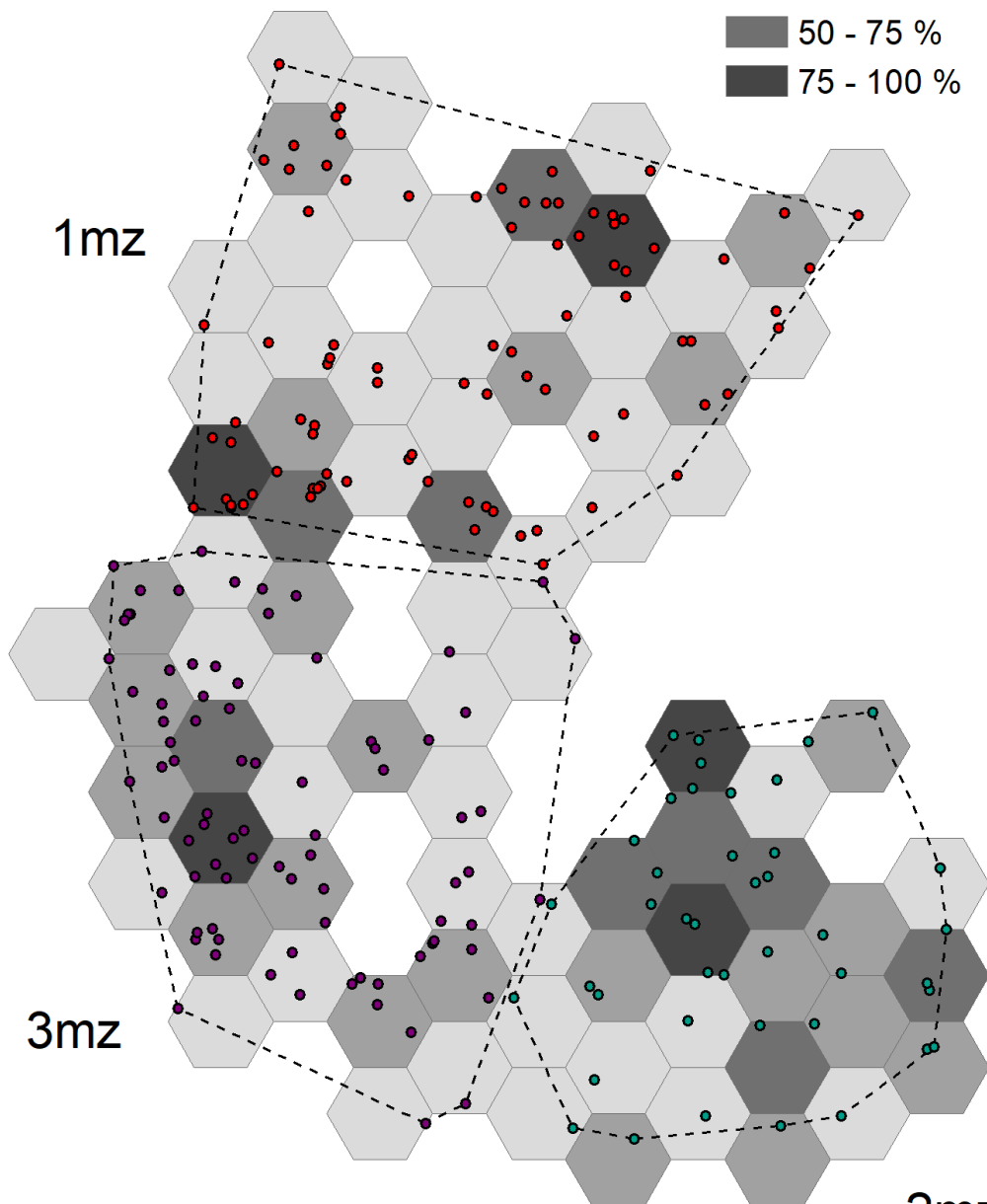
Time spent

0 - 25 %

25 - 50%

50 - 75 %

75 - 100 %



1mz

3mz

2mz



0 75 150 300 Meters

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
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31 10/MEF/SG/DGF/DCB.SAP/SCB), 2011 (N° 274/11/MEF/SG/D GF/DCB.SAP/SCB), 2012 (N°
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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.

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

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

26 **Introduction**

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

30 The area where animals range to meet their survival needs is referred to **as a** home range (Burt
31 1943). **A way to regulate the spacing between neighboring individuals or social units is to defend the**
32 **exclusive use of an area against the intrusion of conspecifics, which we define as a territory and implies**
33 **limited or no overlap between areas occupied by neighboring groups** (Burt 1943, Clutton-Brock 1974,
34 Maher & Lott 1995). When groups defend and exclusively occupy their entire home range, territory
35 and home range coincide (Burt 1943). In the case of territorial species, animals exhibit aggression
36 towards conspecifics attempting to enter a territory (Grant et al. 1992). The strategies of territorial
37 advertisement and defense may influence space use in order to maintain **the** exclusive access to
38 resources (Brown and Orians 1970, López- Sepulcre and Kokko 2005).

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

47 Previous research has shown that in several species, and across different orders, **pair-living** is
48 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, Cowlshaw 1992). The spatial responses to
94 neighboring loud calls can also be influenced by groups' relative dominance and resources availability,

95 as this has been found in howler monkeys (*Alouatta palliata*) (Hopkins 2013). The pattern of emission
96 of such signals within a territory depends on the broadcast distance, the cost of emission, and the
97 behavioral response of the receivers (da Cunha and Byrne 2006, Van Belle et al. 2013). In wild grey-
98 cheeked mangabeys, long distance calls can influence the movements of resident individuals with
99 respect to feeding resources (Brown, this special issue).

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

106 The indri (*Indri indri*) is a pair-living primate that lives in family groups. Each group is
107 composed of two to six individuals, consisting of the reproductive pair and their offspring (Pollock
108 1986). Genetic monogamy is the norm in this species (Bonadonna et al. 2019), and only one case of
109 Extra Pair Copulation (EPC) has been reported between two reproductive individuals of neighboring
110 groups (Bonadonna et al. 2014). Individuals pair for years, most reproductive pairs have been together
111 since the habituation in 2009, although rare cases of take-over or new pairing following the death of the
112 partner have been reported for this species (Bonadonna et al. 2019).

113 Both sexes disperse in this species, and in the population studied in Maromizaha, the offspring
114 remains with the family group for four years, on average (unpublished data). Each group's range is an
115 exclusive and defended area; the home range coincides with the territory and the overlap between
116 neighboring territories is almost absent. The ranging pattern doesn't indicate a constant patrolling of
117 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 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-living 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.

Group code	Study 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	

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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

193 analyze the study periods separately (Bonadonna et al. 2017). Because we wanted to investigate spatial
194 dynamics across time, we prioritized the continuity for each study period, avoiding the loss of
195 biological information. Therefore, we joined the data collected during November and December 2009
196 with 2010, and the data collected in February and March 2013 with 2012.

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

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

213 Every time the focal group emitted a spontaneous advertisement song or was involved in
214 intergroup encounters during the focal observations (Torti et al. 2013) we noted the geographical
215 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):

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

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Where $\cap_{i=1}^n a^i$ is the overall intersection of “n” areas (“n” representing the number of annual territories), and $\prod_{i=1}^n a^i$ is the product of those areas, so that $\sqrt[n]{\prod_{i=1}^n a^i}$ 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.

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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.

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Core area designation and stability

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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.

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: $r_s = 0.4$, $P=0.227$, $N=12$).

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 $10.6 \pm$
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*

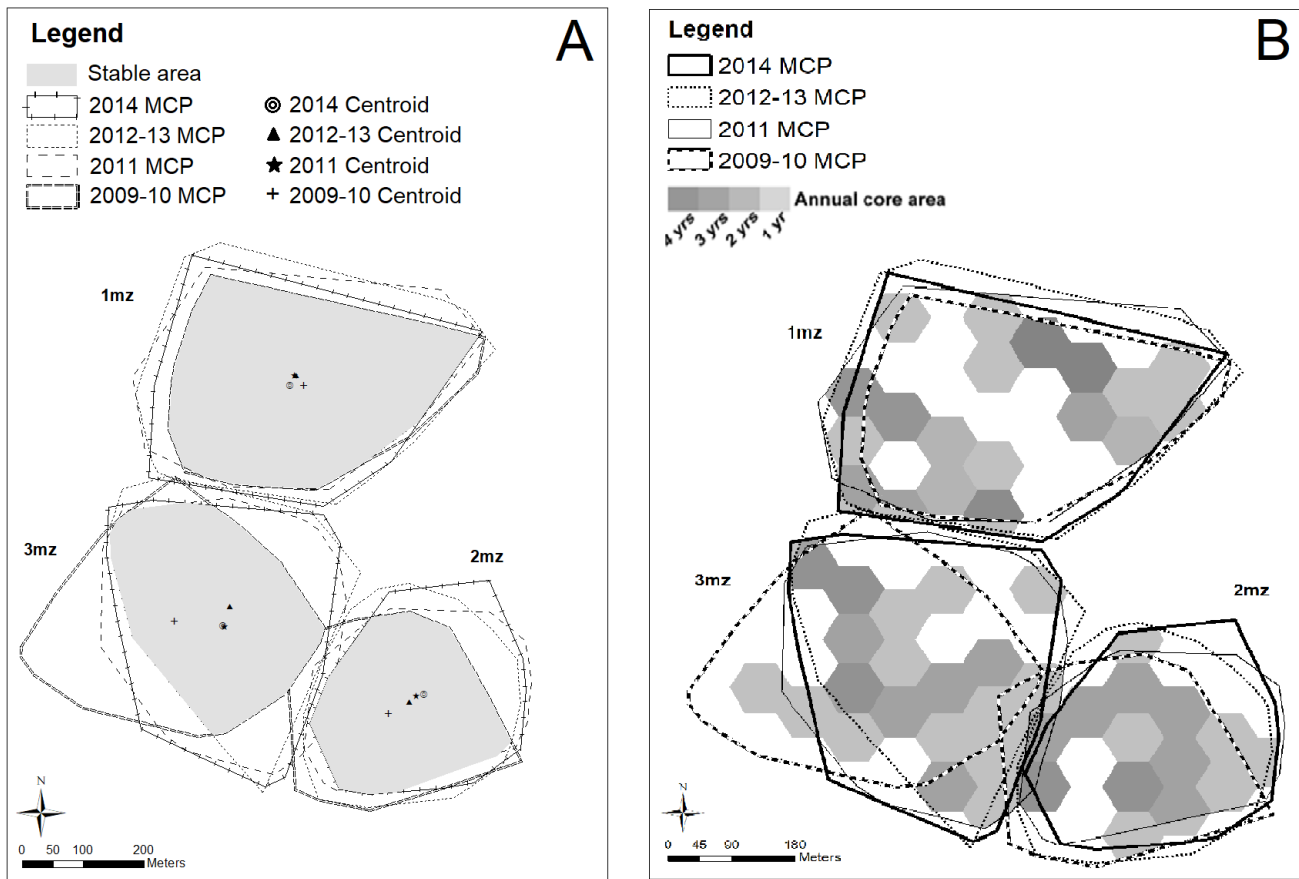
331 According to the Minta Index, we found that the groups 1MZ and 2MZ show high overlap of
332 their territories across time, and group 3MZ is at the upper limit of medium overlap (Table 3). The
333 overall mean percentage overlap between the MCP of a given study period and the overall stable area
334 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 $32\text{m} \pm 24$ (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).

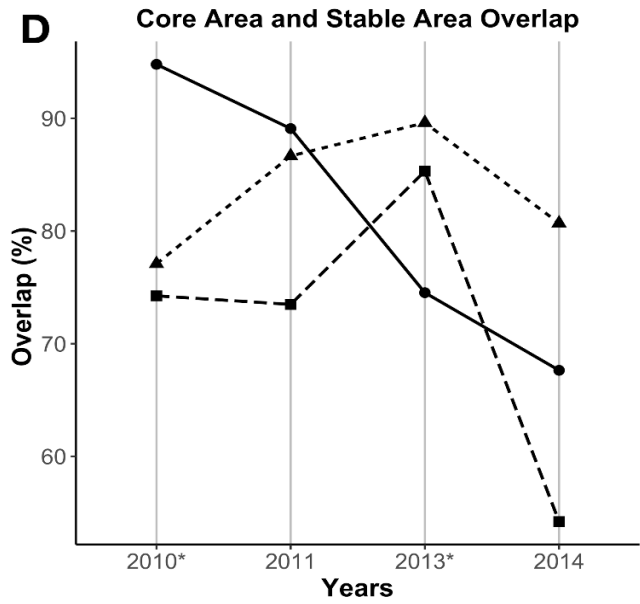
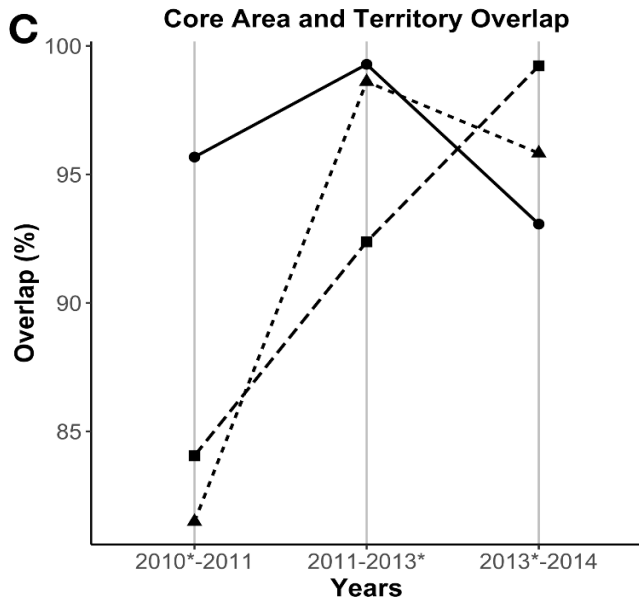
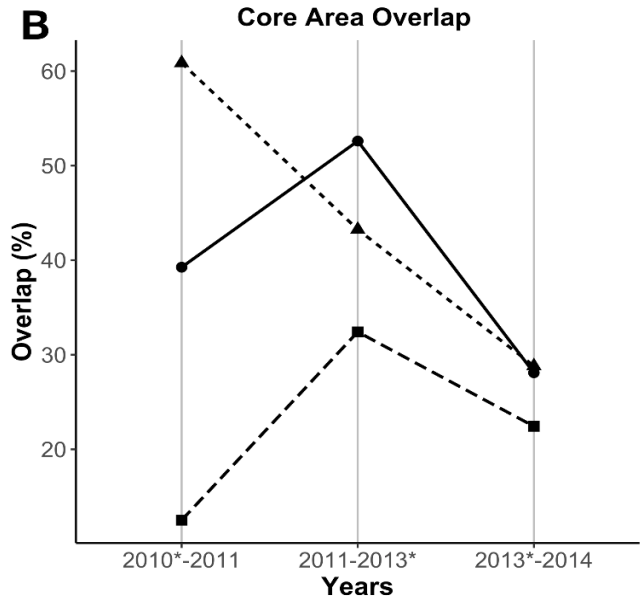
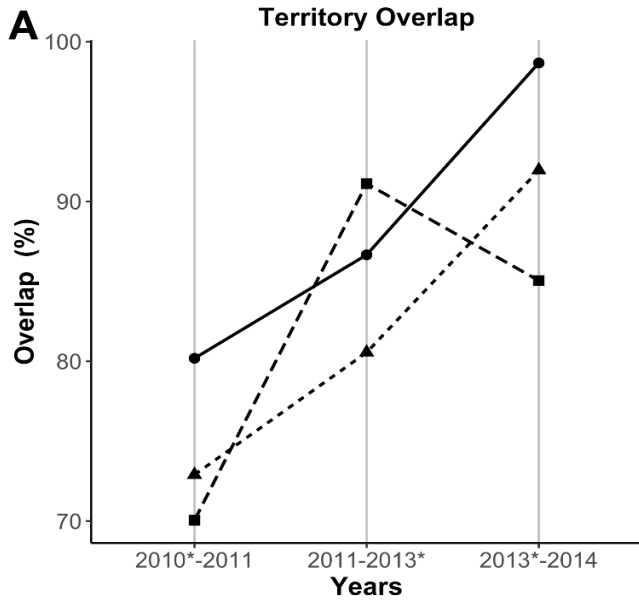
348

349 **Fig. 1. Territory and core area stability for the indri groups 1MZ, 2MZ, 3MZ over four study**
350 **periods (2009-2014) in the Maromizaha forest, Madagascar.** Dashed lines indicate the annual MCP
351 for each group. **A.** Intragroup territories overlap with and centroids for each study period. The gray area
352 represents the overall stable area for each group. **B.** Overlap of the core areas obtained in each study
353 period. Progressive darker shades represent core area shared in multiple study periods (one to four).
354 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.



Group ● 1MZ ▲ 2MZ ■ 3MZ

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 coefficient 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. Territory 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**

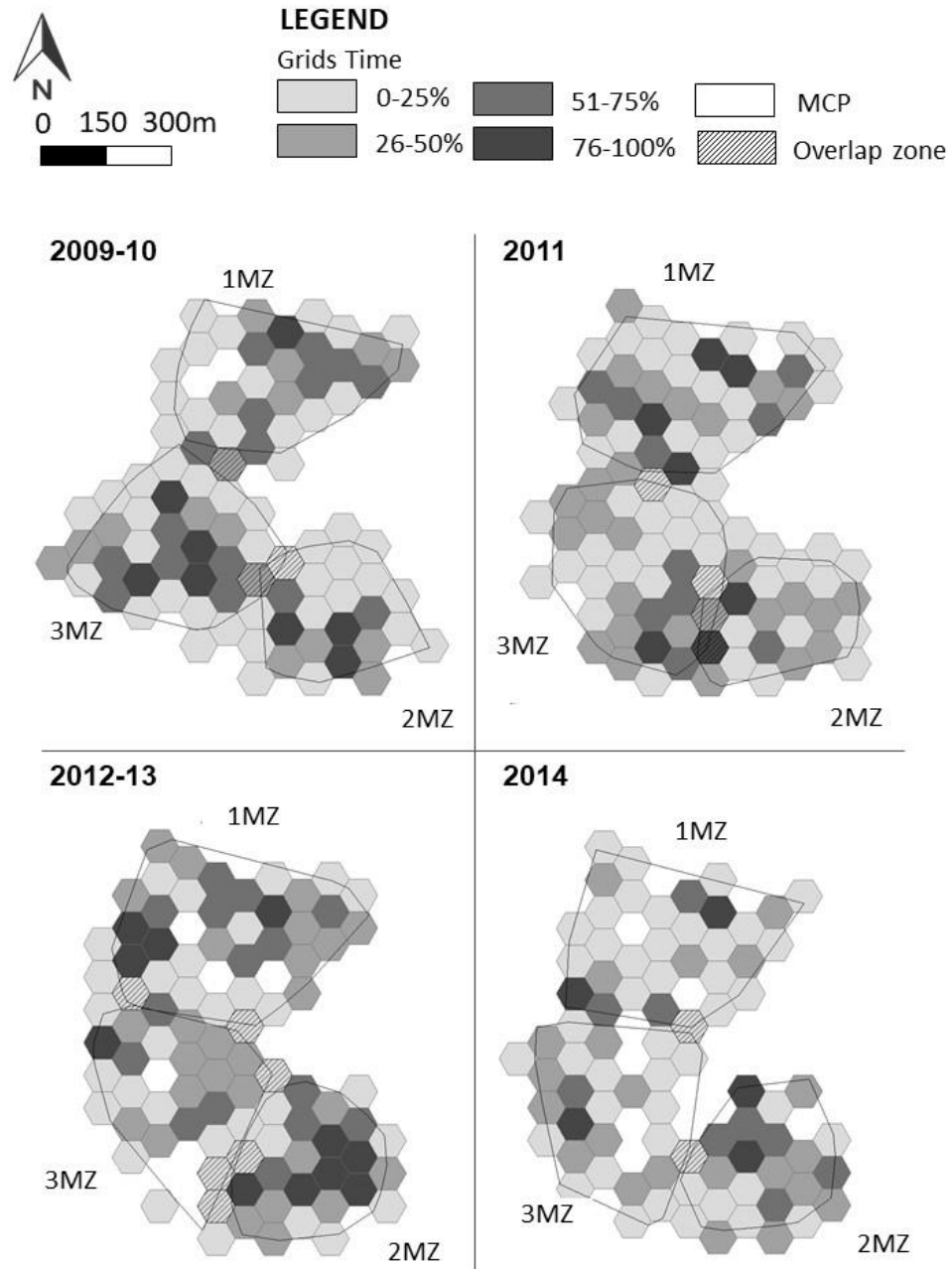
381 We found that areas at higher intensity of use can have a scattered distribution through a
382 group's range and can be located in the center as well as in more peripheral areas of a territory. The
383 same is true for the areas less intensely used by a group in a given year (Fig .3).

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 $22.2 \pm 18.7\%$ 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

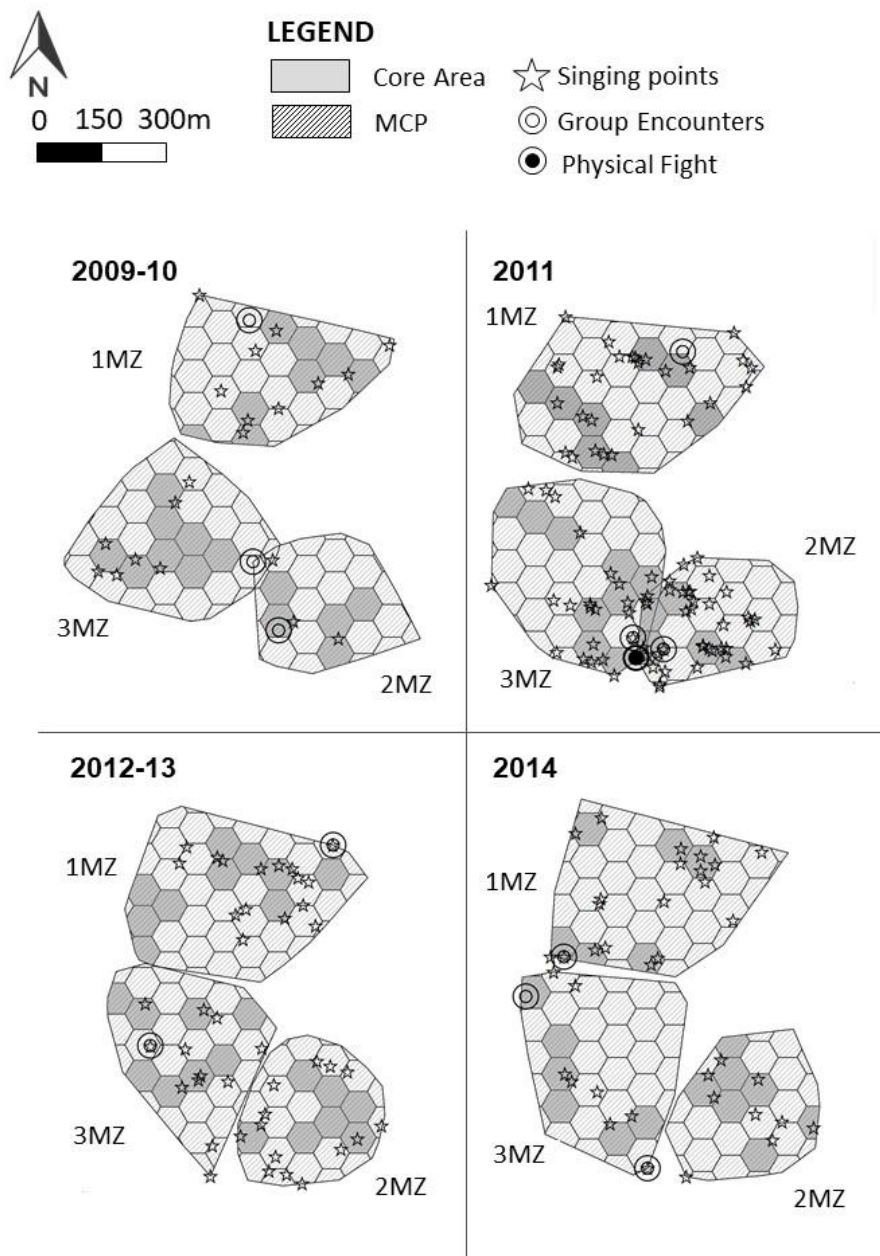
in each indri territory (MCP) during four study periods between 2009 and 2014 (each box represents a

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 $93.3\% \pm 6.5\%$
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 $78.9 \pm 11.2\%$ ($N=12$) 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 $55.9\% \pm 5.2$ ($N=3$) 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 (Kempnaers 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 Muttschler 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 Cunjna 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 klossii*) 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 Cunjna 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.

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582 **Conflict of interests**

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

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