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To cite this article: G. Bonadonna, V. Torti, V. Sorrentino, R. M. Randrianarison, M. Zaccagno, M. Gamba, C. L. Tan & C. Giacoma (2017) Territory exclusivity and intergroup encounters in the indris (Mammalia: Primates: Indridae: Indri indri) upon methodological tuning, The European Zoological Journal, 84:1, 238-251, DOI: [10.1080/24750263.2017.1318184](https://doi.org/10.1080/24750263.2017.1318184)

To link to this article: <http://dx.doi.org/10.1080/24750263.2017.1318184>



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Published online: 18 May 2017.



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Territory exclusivity and intergroup encounters in the indris (Mammalia: Primates: Indridae: *Indri indri*) upon methodological tuning

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(Received 12 December 2016; accepted 5 April 2017)

Abstract

Territorial, socially monogamous species actively defend their home range against conspecifics to maintain exclusive access to resources such as food or mates. Primates use scent marks and loud calls to signal territory occupancy and limit the risk of intergroup encounters, maximizing their energetic balance. *Indri indri* is a little-studied territorial, socially monogamous singing primate living in family groups. The groups announce territory occupancy with long-distance calls, and actively defend their territories from conspecific intruders. This work includes data collected in three forests in Madagascar on 16 indri groups over up to 5 years. We aimed (1) to estimate the extent of territories using minimum convex polygon (MCP), implementing minimum sampling effort requirements; (2) to quantify territorial exclusivity, measuring the overlap between territories; and (3) to evaluate the intergroup encounter rate and to quantify the dynamics of group encounters. Our results showed that indris range evenly within exclusive small territories with no or little overlap. Intergroup encounters are rare (0.05 encounters per day), and are located on the periphery of the territories. Disputes were mostly solved with vocal confrontation and only in 13% of the cases ended in physical fights. This frame underlines a cost-benefit explanation of territoriality, favouring a strategy that efficiently limits overlap and avoids costly intergroup encounters. We hypothesize that territorial behaviour in indri is related to mate-guarding strategy and that vocal behaviour plays a fundamental role in regulating intergroup spacing dynamics.

Keywords: Sampling effort, MCP, territory, intergroup encounters, overlap

Introduction

A territory is an area occupied by an individual or a group, actively defended against conspecifics to maintain exclusive access to resources, usually food or mates (Burt 1943). Territory holders need to adopt strategies to prevent territorial loss and maintain territory exclusivity (Mitani & Rodman 1979; Lowen & Dunbar 1994).

Primates advertise exclusive territory use by emitting keep-out signals, such as loud calls (Whitten 1982; Haimoff 1984; Koda et al. 2012), and defend territories by chasing (Struhsaker 1974; Goldizen 1987) and/or attacking all potential competitors (Manson & Wrangham 1991; Benadi et al. 2008; Mitani et al. 2010; Zhao et al. 2013).

Spatial behaviour and intergroup relationships vary widely among Primates as they are determined by taxon-specific ecological, physiological and social requirements (Jetz et al. 2004). A clear understanding of the mechanisms underlying this variability is important because both spatial and intergroup behaviours represent important determinants of mating system as well as of population density and growth rate (Lazaro-Perea 2001; Glessner & Britt 2005; Spencer 2012).

Indri (*Indri indri*, Gmelin 1788), a diurnal lemur inhabiting the eastern rainforests of Madagascar, lives in socially monogamous family groups (Bonadonna et al. 2014), composed of one adult pair and one to four immature individuals (Pollock

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1979). This lemur is mainly folivorous (Powzyk & Mowry 2003). Indri groups are reported to occupy relatively small territories, whose extension varied according to the study and the site: 17.7 and 18 ha in Analamazaotra Reserve (Pollock 1975), 34 and 40 ha in Mantadia (Powzyk 1997), 27 ha in Betampona (Glessner & Britt 2005). As described by previous studies (Pollock 1979; Powzyk 1997), indris actively advertise their presence and occupancy of a territory (Pollock 1979; Powzyk 1997) by chemical and acoustic signals. They emit long-distance advertisement calls throughout the territory, audible up to 2 km away (Pollock 1986; Powzyk 1997; Torti et al. 2010, 2013; Gamba et al. 2011; Sorrentino et al. 2013). In the indri song, sexes are dimorphic: the overall investment in singing does not differ between males and females (Giacoma et al. 2010), but the tendency to display non-vocal territorial behaviours is more pronounced in adult males (Pollock 1975, 1979). Group encounters are rare: Pollock (1975) observed eight encounters in 15 months, and Powzyk (1997) none during a year of study. However, when two groups meet, they defend their territory ownership by (1) using long vocal interactions or territorial song (Maretti et al. 2010; Torti et al. 2013), and eventually (2) starting physical fights (Pollock 1975, 1979; Powzyk & Mowry 2006). When territorial, monogamous primates live in small groups, are sedentary and invest in far-detectable territorial advertisements (Willems & Van Schaik 2015), they maximize their energetic balance by avoiding territory overlap and physical intergroup encounters. Only one case of extra-pair copulation (EPC) in indri has been reported so far (Bonadonna et al. 2014). On these bases, we hypothesized that indri defend small territories with low overlap in order to reduce EPC opportunities arising by sharing a common part of the territories.

Since the percentage of territorial overlap and the rate of intergroup encounters are related (Bartlett 2003; Willems et al. 2013), our prediction is that group encounters are rare and are located on the boundaries of the territories.

Previous data, collected on only two groups of indri per location for a maximum of 15 months (Pollock 1979; Powzyk 1997), described a low overlap between neighbouring groups, and rare intergroup encounters (Pollock 1975; Powzyk 1997; Glessner & Britt 2005). In the light of the relevant role that territorial dynamics play in indri, it is important to provide quantitative estimates of the territory size and overlap as well as the frequency of intergroup encounters.

The analysis of rare events such as intergroup encounters in indri require a long-term approach

and make it necessary to group data collected during different years, sometimes via different procedures. Furthermore, the sampling effort may vary, creating a methodological issue when estimating territory extent (Haines et al. 2006).

In this work, we address three key questions about indri territories using data collected on 16 groups living in three forests over up to 5 years. First, we provide estimates of the extent of the territories using Minimum Convex Polygon (MCP) including an asymptote-reaching approach; we identify the minimum number of sampling days required to obtain accurate results, allowing comparison among groups under different sampling efforts. Second, we estimate the extent of territorial overlap between neighbouring groups. And, last, we provide a description, rating and location of intergroup encounters. Specifically, we predicted that indri territory sizes are small, territory overlap is low and intergroup encounters are rare.

Methods

Study site and subjects

We collected data on 16 indri groups between 2007 and 2014: seven in Maromizaha, six in Analamazaotra Special Reserve, and three in the Mitsinjo “Station Forestière” (hereafter MSF; Table I). In Maromizaha, habituation of indri groups started in 2009 and animals became used to the human presence by March 2010. The groups inhabit an area of primary forest accessible only when a research permit is granted. Thus, none of the groups has been subjected to mass tourism.

The indri groups in Analamazaotra Special Reserve have been used to human presence at least since the 1990s; groups 1R and 2R are exposed to tourist visits every day. In the MSF, indris have been habituated to humans since 2004 and tourists visit the groups regularly.

Data collection

Individuals were identified by the pattern of their fur patches and were not radio-collared, to avoid any possible effects due to the collar disturbance (Juarez et al. 2011). We followed groups all year round: 67% of fieldwork was conducted during the mating period (September to January) and 33% during the birth season (February to August). The sample size did not allow seasonal comparison; however, the territory estimates obtained from waypoints collected during the two periods did not show differences.

Given the species' diurnal habits (Pollock 1979), we started observations early in the morning (at about

Table I. Comparison of the three study sites (Nicoll & Langrand 1989; Garbutt 1999; Dolch 2003; McConnell & Sweeney 2005; Ratsimbafy et al. 2008; Mittermeier et al. 2010).

	Maromizaha	Analamazaotra Special Reserve	Analamazaotra Station Forestière (Mitsinjo)
Management	New Protected Area (NAP) managed by Group d'Etude et de Recherche sur les Primates de Madagascar (GERP) (since 2008)	Andasibe-Mantadia National Park; managed by the Ministère de l'Environnement et des Forêts (since 1970)	Reserve managed by Association Mitsinjo (since 2003)
Coordinates	18°56'S, 48°27'E	18°56'S, 48°25'E	18°56'S, 48°24'E
Area (ha)	1880	810	710
Altitude (m)	800–1200	900–1040	920–970
Type	Primary and secondary mid-altitude evergreen rainforest	Secondary mid-altitude tropical evergreen rainforest	Secondary mid-altitude tropical evergreen rainforest and restored habitat
Annual rainfall (mm)	1779	1700	1700
Endemism rate	77%	No data available	No data available
Vegetation type	<i>Tambourissa</i> (Monimiaceae), <i>Weinmannia</i> (Cunnoniaceae), <i>Cryptocaria</i> (Lauraceae), <i>Homalium</i> (Salicaceae), <i>Eugenia</i> (Myrtaceae), <i>Ocotea</i> (Lauraceae), <i>Uapaca</i> (Phyllantaceae),	<i>Tambourissa</i> (Monimiaceae), <i>Weinmannia</i> (Cunnoniaceae), <i>Cryptocaria</i> (Lauraceae), <i>Dalbergia</i> (Fabaceae), <i>Symphonia</i> (Clusiaceae), <i>Vernonia</i> (Asteraceae)	<i>Tambourissa</i> (Monimiaceae), <i>Weinmannia</i> (Cunnoniaceae), <i>Dalbergia</i> (Fabaceae), <i>Ravensara</i> (Lauraceae), <i>Symphonia</i> (Clusiaceae)
Total number of lemur species	13	12	11
Diurnal lemur species	Diurnal: <i>Indri indri</i> , <i>Varecia variegata</i> , <i>Propithecus diadema</i> , <i>Hapalemur griseus</i> , <i>Eulemur rubriventer</i> , <i>Eulemur fulvus</i>	Diurnal: <i>Indri indri</i> , <i>Hapalemur griseus</i> , <i>Eulemur rubriventer</i> and <i>Eulemur fulvus</i> (<i>Varecia variegata</i> and <i>Propithecus diadema</i> were not introduced yet when we collected the data)	Diurnal: <i>Indri indri</i> , <i>Hapalemur griseus</i> , <i>Eulemur rubriventer</i> , <i>Eulemur fulvus</i>
Logging status	The management planning of traditional activities was established in 2008. Furthermore, deforestation is still practiced in the forest border for illegal logging, charcoal and agriculture land.	In the late 1990s and early 2000s the natural forest of Analamazaotra was illegally logged at an alarming rate; charcoal production from native timber led to several forest fires that added to the destruction, but nowadays illegal activities have been stopped.	Illegal logging and hunting using snares are very rare.
Eco-tourism area	Yes	Yes	Yes

06:00), when individuals woke up, and we followed the groups until they became inactive at about 13:30. In this way, the daily sampling rate remained constant. However, observation hours vary during the sampling, according to group detectability. In order to verify whether differences existed between study groups, we estimated mean annual observation hours and we applied a non-parametric test (Kruskal–Wallis H test).

We recorded the ranging behaviour using the focal group sampling method (Altmann 1974), so each waypoint represents the centre of the group members. This study is based upon direct foot field observations of VT, GB, VS and three research guides trained since 2009 as field assistants. Researchers contributed to the data set only when they reached 95% agreement with the data collected by experienced research guides. Indris' ranging pattern

showed progressive directional displacements (travel routes) between successive “stationary areas” or “target areas” (Lair 1987; hereafter, stationary areas). In order to select biologically independent locations (Lair 1987), we considered stationary those areas responding to all of the following criteria: (1) the animals arrived at the location after having interrupted their previous activity; (2) the group stayed around for at least 5 minutes; and (3) animals had moved at least 20 m from the last location (see Asensio et al. 2011). In order to standardise the method of waypoint collection between different observers, we used the Garmin handle global positioning system (GPS) distance calculator. In stationary areas animals stopped for lasting activities, such as feeding, resting or sleeping; individuals moved vertically or horizontally on the same tree, or even jumped from adjoining trees, but the group

maintained cohesion until starting a new directional displacement. Whenever the group reached a new stationary area, we recorded the coordinates of its spatial centre on a hand-held global positioning unit (GPS Garmin MAP 76CSX) with an accuracy of 5 m.

Data analysis

We imported GPS waypoints into ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA). We converted all GPS waypoints into decimal degrees and then into geographic

information system (GIS) shape files projected in UTM WGS_1984 39S. We obtained 2328 GPS waypoints for 643 days (Table II); we analysed annual records independently to limit size overestimation caused by territory shifts over time. The only exception consisted in grouping GPS data collected in Maromizaha in August 2013 with those recorded in October–December 2012 (hereafter, 2012). We relied on the evidence that a previous study did not find differences in ranging throughout the year (Pollock 1979). In this way, we did not have to exclude waypoints, which would have resulted in the loss of biological data. To identify the territories

Table II. This table reports site name, code of the indri group, years of sampling, total number of sampling days, total number of waypoints recorded, observation: mean duration of daily observation in hours N ind: number of individuals composing the group according to year. The italic codes represent data sets that we did not utilize for quantitative territory size estimates.

Site	Group	Year	No. days	No. waypoints	Observation	Group size
Maromizaha	1MZ	2010	25	92	5:42 ± 1:47	3
		2011	34	122	6:41 ± 1:24	4
		2012	45	141	6:22 ± 1:27	4
		2014	32	86	4:22 ± 1:12	3
	2MZ	2009	16	54	04:58 ± 1:46	2
		2010	17	55	4:51 ± 1:28	3
		2011	23	90	6:41 ± 1:01	2
		2012	44	146	5:36 ± 1:25	2
		2014	17	42	4:11 ± 0:50	3
	3MZ	2009	21	72	5:51 ± 1:03	3
		2010	19	56	5:25 ± 2:20	3
		2011	38	149	5:46 ± 1:22	4
		2012	27	73	5:48 ± 1:01	3
		2014	34	83	5:14 ± 1:16	4
	4MZ	2014	11	34	5:21 ± 0:32	4
	8MZ	2014	23	72	4:36 ± 0:55	4
	9MZ	2014	14	54	4:48 ± 1:57	4
10MZ	2014	23	92	4:49 ± 1:15	3	
Analamazaotra	1R	2005	8	23	5:27 ± 0:49	4
		2007	5	26	5:36 ± 3:13	4
		2008	5	16	5:35 ± 1:10	4
	2R	2005	12	31	6:26 ± 1:46	6
		2007	10	71	5:24 ± 1:35	5
		2008	7	25	5:21 ± 1:46	5
	3R	2005	13	31	5:25 ± 1:17	5
		2006	9	24	5:22 ± 1:22	5
		2007	8	41	5:26 ± 2:03	5
	5R	2008	9	33	5:31 ± 2:03	5
		2005	5	14	5:09 ± 1:38	2
		2007	4	27	6:40 ± 0:18	3
	6R	2008	5	25	5:46 ± 0:34	4
XR	2006	5	16	04:44 ± 0:15	2	
Mitsinjo	ASF	2005	10	33	5:36 ± 1:18	4
		2007	8	51	5:39 ± 1:06	4
		2008	4	14	6:42 ± 0:50	4
	WSF	2005	5	19	5:11 ± 1:55	2
		2007	4	24	4:42 ± 0:51	3
	YSF	2005	8	33	5:38 ± 1:58	3
		2007	7	80	5:39 ± 1:13	4
		2008	29	158	6:42 ± 1:24	4
	TOTAL		643	2328		

of indri groups, we built annual MCPs for each group using ArcGIS extension package Hawth's Analysis Tools (version 3.27; Beyer 2004) without applying any outer point peeling technique (MCP100) (Figure 1).

Sampling effort and territory size

We used MCP100 to calculate the annual territory size in hectares (ha). To analyse the effect of the sampling efforts on territory size estimates, we considered the number of sampling days because the number of waypoints changes among days.

Estimates of territory sizes by MCP strongly depend on sample size (Seaman et al. 1999; Powell 2000; Börger et al. 2006; Laver & Kelly 2008). A recommended way to validate territory estimates is to verify whether the sampling effort is large enough so that the territory size reaches an area-curve asymptote (Seaman et al. 1999; Powell 2000; Girard et al. 2002; Haines et al. 2006).

To assess the cumulative effect of daily data collection on territory size estimates obtained with MCP,

we selected a subsample of seven data sets corresponding to the annual territory of the five groups with more records (Table III). We plotted: (1) the daily coverage increment expressed as a percentage of total territory size (IC); and (2) the decrement of daily rate in territory size increment (DC) as a function of the number of sampling days with at least three waypoints. We built the curves as described below:

1. Coverage increment curves (IC): Theoretically, sampling a group on successive days or during an interval may affect the territory estimates because the indris' ranging in a day is potentially dependent on their position recorded the day before. To reduce this effect, we used data collected daily to estimate the area covered in a day. We then randomized the sampling days (and the respective areas) to calculate the percentage of the total size to the number of sampling days independently from their temporal sequence. We then plotted the mean percentage of annual territory size produced by 100,000 randomizations (Random module of Python 2.7) as a

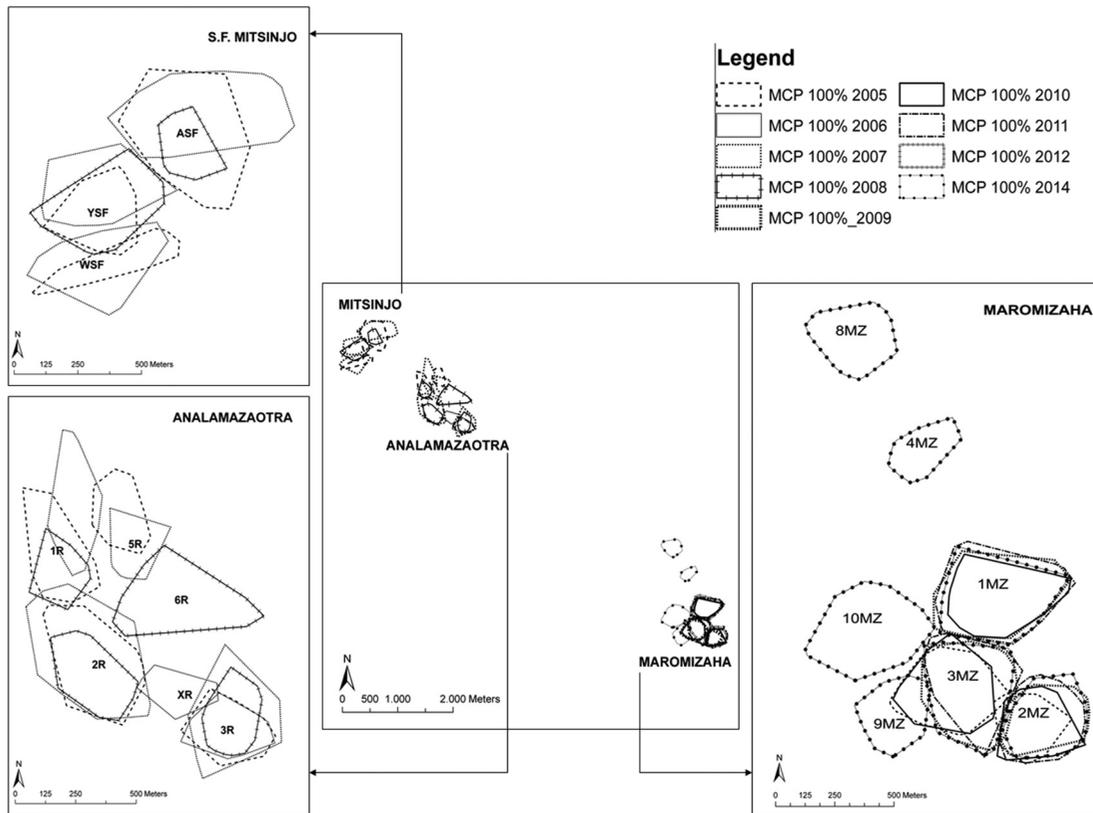


Figure 1. Annual territories of the 16 indri groups in each site: six groups in the Analamazaotra Special Reserve, three groups in the Mitsinjo Station Forestière, and seven groups in the Maromizaha forest. Polygons represent the minimum convex polygons (MCPs) at 100%. The legend box identifies the different lines used to draw annual MCP, allowing the relative location of groups' territory in the same year, as well as the area occupied by a group through the years, to be distinguished.

Table III. Group codes and relative year of sampling of the seven data sets used to compare different estimate methods of the territory size: MCP, size corresponding to the MCP100% built including the total number of sampling days per each year; MCP_r, size obtained by randomization of daily data sets with a minimum of three waypoints; MCP_i, size made up to 100% starting from the size obtained with MCP_r at 8 days corresponding on average to 74% of total coverage; MCP_d, size made up to 100% starting from size simulated at 16 days of sampling, corresponding on average at 92% of total territory size. We reported the percentage difference between territory size obtained with MCP and the size simulated with the methods MCP_r, MCP_i and MCP_d. Mean and SD are also indicated.

Group	Year	Homerange size (ha)						Difference of size between estimate methods (%)		
		No. days	MCP	No. days (> 2 waypoints)	MCP _r	MCP _i	MCP _d	MCP _r -MCP	MCP _i -MCP	MCP _d -MCP
1MZ	2010	29	12.36	21	12.19	12.35	12.47	1.4	0.1	0.9
1MZ	2011	34	15.47	25	15.40	15.77	15.38	0.5	1.9	0.6
1MZ	2012	42	17.47	36	16.78	15.12	15.80	4.1	13.4	9.6
2MZ	2011	23	9.55	22	8.73	9.41	9.38	9.3	1.4	1.8
3MZ	2011	38	14.72	35	14.44	13.36	13.41	1.9	9.2	8.9
10MZ	2014	23	14.62	18	14.01	14.98	15.23	4.3	2.5	4.2
YSF	2008	29	12.20	27	12.20	11.13	11.52	0.0	8.8	5.5
mean			13.77		13.39	13.16	13.31	3.1	5.3	4.5
SD			2.60		2.63	2.34	2.36	3.2	5.1	3.7

function of the number of sampling days available for each year (SM1).

2. Decrement rate curves (DC): To obtain the curves, we chose values obtained by the randomization of up to eight sampling days for each case. We calculated the daily difference in size by subtracting the average absolute territory size given by randomizations at day X_i from the mean territory size at day X_{i+1} . Then, we expressed this difference as the percentage of the mean territory size at day X_i . To find the best-fitting function representing the trend of DC, we used LAB Fit Curve Fitting Software 7.2.48 (de Silva & de Silva 2011) resulting in the exponential function:

$$Y = A * X^B \quad (1)$$

where X is the number of days of sampling, Y is the percentage of increment in size from the previous day of sampling, and A and B are the two constant parameters of the function calculated for each data set (SM2).

We then applied Equation (1) and simulated the decrement up to the total number of days available for each data set (SM2).

Finally, we considered the seven selected data sets big enough to give a reliable estimate of territory size with MCP100, and we compared territory size estimates based on the entire number of the sampling days respectively with:

3. MCP_r: the territory size was the estimates at 100% of the territory obtained with randomization of daily data sets.
4. MCP_i: territory estimates obtained enhancing up to 100% the territory size resulting from randomization of eight sampling days considered

equivalent to the average percentage given by the IC at day 8.

5. MCP_d: a three-step process. First, we calculated the DC parameters from the estimates in hectares obtained with the randomization at 8 days up to 16 days; second, we applied the parameters simulating a size based on eight sampling days that corresponded to DC values below 1.6% and corresponding on average to 92% of the territory extent; third, we made up the estimates up to 100%.

To compare the results obtained with MCP100 and the different predictive methods, we ran a Wilcoxon signed rank test (IBM SPSS Statistics 22) reporting the number of cases N as well as the Z and p values (confidence level at 95%).

The results obtained from the analyses on the subsample allow us to identify the minimum requirement to consider a data set reliable to calculate the extent of the territory size. We included only years with a minimum of eight sampling days, with at least three waypoints, obtaining a total of 22 cases for 10 groups to calculate the mean territory size (Table III). In the case of less than 16 sampling days available, we applied the DC correction (MCP_d) so that our estimates reach at least 90% of MCP100 for all data sets. Once we obtained the territory size, and acknowledging the number of individuals in an indri group for a certain year, we were also able to calculate the population density.

Group spacing and intergroup encounters

We detected the presence of overlap between neighbouring territories in the same year, and we calculated the percentage of overlap between neighbouring

territories in those cases for which the sampling effort was sufficient to have an accurate representation of territories (Table IV).

We also plotted the intergroup encounter locations together with annual MCPs. We defined intergroup encounters as whenever two groups got in visual contact and displayed vocal or physical aggression against each other. Because of the chaotic nature of the event, we recorded all the vocalizations emitted and described the general dynamic of the encounter, documenting any eventual physical contact or aggression between individuals, using an *ad libitum* sampling method (Altmann 1974). We considered the encounter concluded when one or both groups moved away from the encounter location.

As the first step, we quantified the intergroup encounters recorded over the years, and we calculated a daily rate occurrence as well as the percentage of cases with vocal confrontation or physical fights. Only for those cases in which we have a reliable description of the territory borders (16 encounters), we quantified the distance of the encounters to the boundary. We considered an internal buffer of 15 m

Table IV. Table IV reports codes of indri groups; year of sampling; total annual number of sampling days; total number of sampling days with a minimum of three waypoints; territory size estimates using Minimum Convex Polygon (MCP) 100% (ha), (*) estimates corresponding to MCPd (see also Table III) applied when N days of data set was lower than 16; boundary length (BL); and group size for each year.

Group	Year	No. days total	N days > 2 wp	Territory size (ha)	BL (m)	Group size
1MZ	2010	25	21	12.36	1395	3
	2011	34	25	15.47	1548	4
	2012	45	36	17.47	1607	4
	2014	32	13	15.03	1559	3
2MZ	2009	16	9	6.63	978	2
	2010	17	9	8.26	1114	3
	2011	23	22	9.55	1114	2
	2012	44	20	10.18	1169	2
3MZ	2014	17	9	9.57	1149	3
	2009	21	12	12.25	1314	3
	2010	19	11	12.09	1307	3
	2011	38	35	14.72	1396	4
4MZ	2012	27	12	12.94	1434	3
	2014	34	16	13.91	1444	4
	2014	11	8*	5.05	nd	4
	2014	23	13	8.52	1096	4
8MZ	2014	14	9*	8.01	nd	4
10MZ	2014	23	18	14.62	1442	3
2R	2005	12	8*	17.57	nd	6
	2007	10	10*	25.91	nd	5
ASF	2007	8	8*	25.79	nd	4
YSF	2008	29	29	12.20	1387	4
tot		522	310			
mean				13.10	1321	
SD				5.31	186	

from the outlined MCP to identify the ones falling on the limit of the territory.

Finally, we analysed the ranging pattern associated with group encounters. We quantified the length of the displacement preceding and following an encounter, and we recorded the times when a group moved towards the encounter location, a group moved away from the location after the encounter, or the group did not change location during the whole day of observation.

Results

Sampling effort and territory size

A Kruskal–Wallis H test showed that there was no statistically significant difference in the daily distribution of observation hours (Table II) between the study groups ($N = 40$; $H = 14.580$; $df = 15$; $p = 0.482$), excluding a potential bias in our data.

How a group ranges in its territory can influence the sampling effort required to have a representative estimation of the total territory size. On average, we found that in the 12% of the total days of observation a group stayed in a single stationary area, and in 18% a group moved between only two stationary areas. These data point out the challenge to obtain independent waypoints with a given sampling effort.

Indri movements within the territory are evenly distributed. When we considered the ranging pattern of group YSF (group Y of the S. F. Mitsinjo) recorded in 2008, during 13 successive days at Mitsinjo, we found evenly distributed tracks between the centre and the MCP boundaries such that a group takes 2 weeks to range in the whole territory (Figure 2).

Plotting the IC as a function of the number of sampling days, we saw that territory size increased with the increase in sampling effort. We found that MCP estimates based on 8 days of sampling corresponded to a mean area coverage of 68–81%, while 16 days corresponded to 86–100% (SM2). We found that the area obtained at 8 days of sampling represents on average 74% of the territory size. We applied this result to obtain the territory size using the method of MCP (Table III).

In the selected annual data sets (Table III), decrement in territory size values at 8 days of sampling ranged between 4.0 and 5.7%, and corresponded to an area coverage of 67–81%; at 16 days, the DC reached values between 1.1–1.6% (on average 1.33%, SM1) and corresponded to an area coverage of 88–97%, on average 92% (SM2).

The mean difference % (\pm standard deviation, SD) between the territory size obtained with the MCP100 and the randomizations (MCP) is 3.1% (± 3.2), with a maximum value of 9.3% (Table III);

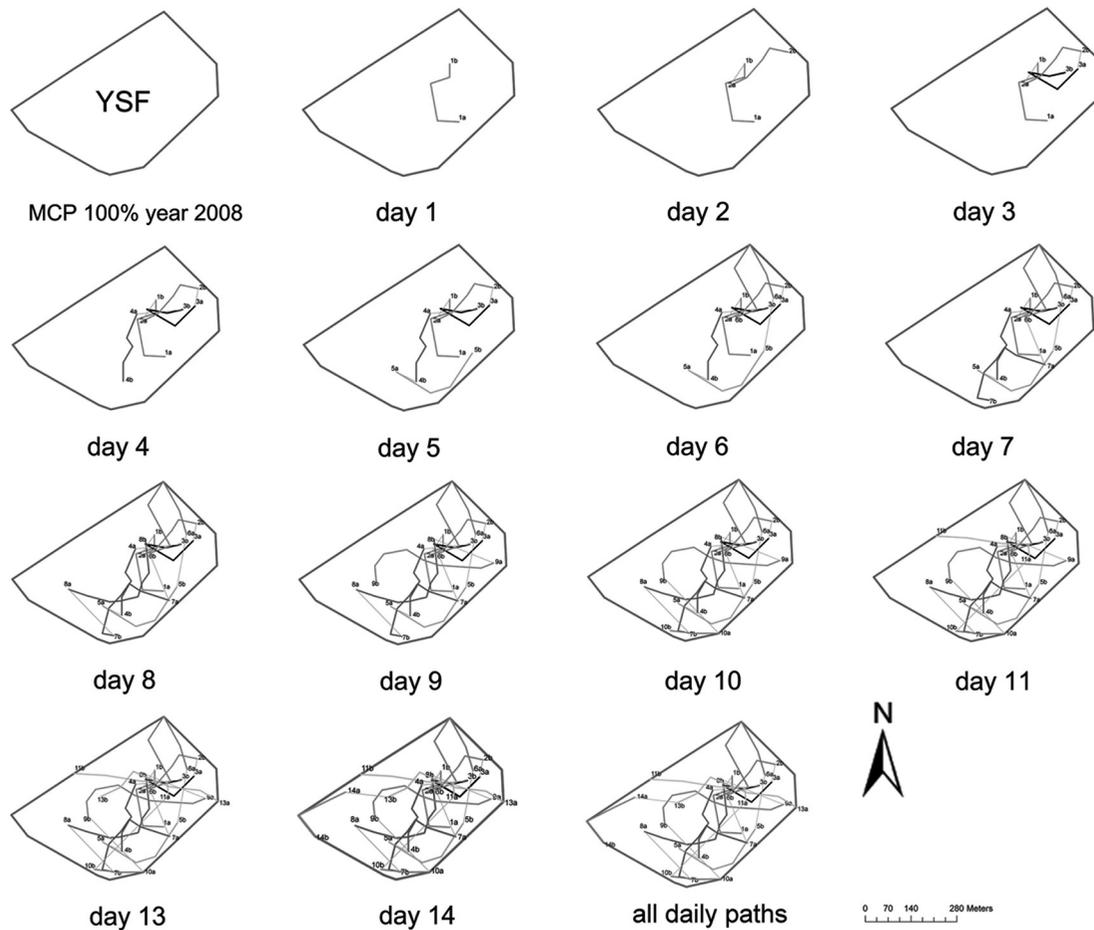


Figure 2. The ranging pattern of the group YSF (Mitsinjo Station Forestière) in 2008. We show the daily travel paths of the group YSF during 13 consecutive days (except for missing data of day 12). The group YSF travelled from the core of the territory to the northeastern boundary (from day 2) and then moved to the southwest (from day 8). The group covered the whole territory over 13 days.

the size estimates we obtained are significantly different between the two methods (Wilcoxon Signed Rank test: $N = 10$; $Z = -2.201$; $p = 0.028$).

The mean percentage difference of territory sizes obtained with MCPi from the sizes obtained with MCP100 is 5.3%, ranging between -13.4% and 2.5%, which means that this method resulted in estimates that did not always reach at least 90% of MCP (Table IV). Territory sizes were not significantly different from that obtained with MCP100 (Wilcoxon signed ranks test: $N = 7$; $Z = -1.183$; $p = 0.237$).

The mean percentage difference of territory sizes with MCPd from the sizes resulting with MCP100 is 4.5% (+ 3.7), ranging from -9.6% to 4.2%. The difference is always less than 10%. Therefore, size estimates always exceeded 90% of the ones obtained with MCP100 (Table II). Further, this method resulted in the lowest variability between data sets (range = 8.6) compared to the other methods. Even if differences were mostly negative, they were not

significantly different from the ones obtained with MCP100 (Wilcoxon signed ranks test: $N = 7$; $Z = -1.690$; $p = 0.091$). MCPi and MCPd estimates were not significantly different (Wilcoxon signed ranks test: $N = 7$; $Z = -0.845$; $p = 0.398$).

Considering the initial data set, we were able to provide estimates of the territory size in 22 cases including 10 indri groups; in five cases, the size was obtained applying MCPd correction. We found a mean annual territory size of 13.10 ± 5.31 ha, ranging from a minimum of 5.05 ha for the group 4MZ in 2014 (Maromizaha) and a maximum of 25.91 ha for the group 2R in 2007 (Special Reserve of Analamazaotra) (Table IV). These results correspond to an average annual population density of $27.7 (\pm 4.0)$ individuals and $8.4 (\pm 1.0)$ groups per km^2 in Maromizaha; $26.7 (\pm 10.5)$ individuals and $4.8 (\pm 1.3)$ groups per km^2 in Analamazaotra; and $24.2 (\pm 12.2)$ individuals and $6.1 (\pm 3.0)$ groups per sqkm in Mitsinjo.

Group spacing and intergroup encounters

MCPs in Figure 1 show the overall spatial distribution of the groups: MCP boundaries of neighbouring groups are usually side by side, and overlap between territories in the same year is very rare. Looking for overlap between neighbouring territories considering the 22 accurate estimates of annual extent reported in Table IV, there are 13 possible contact zones between neighbouring groups, all in Maromizaha. Instead, from a quantitative analysis we found an overlap of more than 1% only in two cases: in 2009 when the territory of group 3MZ overlapped with group 2MZ for 1.54% of its extension, and in 2011 when the territory of group 3MZ again overlapped the territory of group 2MZ, by 3.00%.

Intergroup encounters are also rare: during 36 months of field observations on 16 groups, we only recorded 30 encounters (estimated rate 0.05 encounters per day or one encounter every 20 days). During encounters, males typically sat, stared at each other, marked and vocalized from branches in the upper parts of the canopy. Females usually stayed in the background and contributed to vocal emissions together with all the other group members. Disputes lasted from a few minutes to over 2 hours and were always accompanied by long vocal exchanges characterized by alternating songs between the two groups. Other vigilance and aggressive vocalizations (see Maretti et al. 2010), particularly kiss, wheeze, grunt, roar and honk, were

emitted in this context. After a dispute resolution, the adult male (or more adult males) re-joined the female and resumed their normal ranging and feeding activities.

Of the 30 reported encounters, 26 were solved with territorial songs, and four ended in physical fights (Figure 3). During the physical fights, males fought by resorting to reciprocal bites and scratches. In two cases, an adult male fell to the ground; on the two other occasions a contending male was injured.

Considering that the diameter of a territory is on average 400 m, the encounters are located at the periphery: 60% of encounters are within 15 m of the MCP perimeter, and in 93% of cases within 60 m. The mean distance from the encounters to the border is 22 ± 27 m, ranging between 0 and 82 m.

Of the 16 cases included in the quantitative description of the encounter locations, 14 were solved with vocal fights. In 43% of these, a group was on the periphery of the territory before the encounter took place and stayed at the periphery afterwards; in 36% of cases it moved towards the centre after the encounter; in 13% of cases the group moved to the boundary before the encounter and remained in the same area afterward.

In the only case of encounter in an inner zone, the group subsequently stayed in the centre of the territory. This last encounter occurred in 2012 between groups 3MZ and 9MZ. It is notable that in December 2011 two individuals of these groups

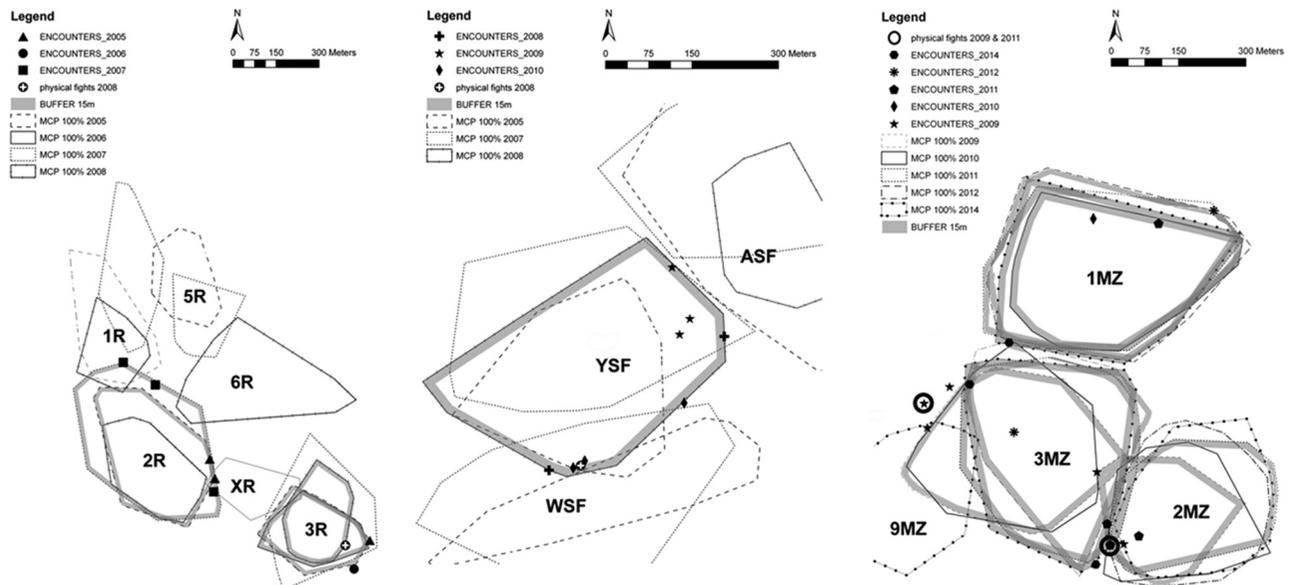


Figure 3. Intergroup encounters observed from 2005 to 2014 in the three sites. Different symbols represent the encounter locations and minimum convex polygons (MCPs) according to the year. The grey shaded buffers represent the 15 m wide area of the annual territorial boundaries (we highlighted the MCP boundary only for the years in which we recorded an encounter).

were involved in an EPC event that might be in some way related to an important loss of territory and shift of the group 3MZ with respect to the group 9MZ in the same year (Bonadonna et al. 2014). Therefore, we can assume that the territories of two groups might be in a transition phase.

In cases of physical fights, we have the displacement data of the focal group after the encounters in two cases out of four: in one case, the group continued to range on the limit of the territory; in the other case, the group moved towards the centre of the territory.

Discussion

With this multiannual work, we provided a quantitative description, based on a methodological validation, of the territory size of indri. We gave insight into the mechanisms that regulate territorial dynamics at the intergroup level as spatial overlap, intergroup encounters and boundary defence.

Effect of the sampling effort and territory size

Our results show that indri ranges evenly within exclusive territories with no or little spatial overlap. Indris can cross their entire territory in few minutes, but they normally move few times during the day. This sedentary attitude limits the number of temporally independent data that can be collected. Using the approach of biological rather than temporal independence allowed us to maximize the biological information in our data, as well as to ensure an adequate sample size (Swihart & Slade 1985; Lair 1987).

The exclusive territories, the sedentary habit and the following small data set of biologically independent waypoints make MCP an appropriate method to estimate the extent of indri territory size (Girard et al. 2002; Row & Blouin-Demers 2006; Downs & Horner 2008). However, several empirical and simulated studies comparing home range and territory size estimators suggest comparing MCP results with those obtained by other methods (Worton 1987; Boulanger & White 1990; Powell 2000; Kenward et al. 2001; Laver & Kelly 2008). Hence, we took the option to run asymptote analyses and to evaluate the accuracy of estimates obtained with different data sets (Girard et al. 2002; Börger 2006). Our models provide further evidence that the sampling effort affects estimates of the territory size evaluated with MCP, as previously highlighted in other species (Powell 2000; Girard et al. 2002; Signer et al. 2015).

Concerning indri, we found evidence that 8 days of sampling are enough to obtain an accurately

simulated territory size of an indri group. The DC method is the one that provides the most accurate results, reaching at least 90% of the total size. The main strength of this method is the independence from the final territory size excluding the effect of the sample size, whereas its limitation is that it does not allow the spatial location of the boundaries of a territory.

Implementing a method that can estimate and allow increasing the accuracy of territory size estimates based on the number of sampling days not only allows the comparison of heterogeneous data sets, but also provides important information about the minimum requirements in term of sampling effort. This is a critical issue considering the high investment of resources required in field studies, especially from a long-term perspective (Girard et al. 2002). We demonstrated that when using MCP no fewer than 16 days of sampling are required to reach at least the 90% of territory extent, and so to obtain both an accurate size estimation and a reliable spatial representation of the territorial boundaries.

Territory exclusivity and defence

Indri represents an interesting model to study territory exclusivity and defence: among the few territorial folivorous primates, it is the one with the smallest range size (Cheney & Seyfarth 1987), it is monogamous, and it makes use of songs to communicate at intergroup level. A key step for understanding which factors play a role in determining the territory sizes in indri will be to learn more about habitat quality, which is known to dramatically affect territory size in other primates (*Symphalangus syndactylus*: Chivers 1974; *Presbytis femoralis*: Bennett 1986; *Hoolock leucomedys*: Zhang et al. 2014)

The nocturnal white-footed sportive lemur (*Lepilemur leucopus*) is an example of a folivorous, vocal, territorial primate that limits territory overlap and contact with conspecifics. In this species, territory quality is related to territory size and defence, and the authors hypothesize a mechanism of resource defence as mating strategy and the use of latrine as mate defence (Dröscher & Kappeler 2013, 2014a,b).

We claim that the degree of territory overlap between neighbouring groups (Pollock 1979, 1986), which is rare and considerably lower than the average overlap reported by Lukas and Clutton-Brock (2013) for 26 socially monogamous primates (21%), is related to the mating system of this species. Even if in other monogamous species the overlap can be higher than in indri, they still tend to avoid encounters with neighbours. A study on masked titi monkeys (*Callicebus personatus personatus*) reported

an overlap between neighbouring territories of 20%, but intergroup encounters were rare and exclusively vocal (Price & Piedade 2001).

A similar overlap between neighbouring territories can be found in carnivorous, territorial cooperative breeders: meerkats (*Suricata suricatta*) show on average 20% of overlap (Jordan et al. 2007) and regulate the avoidance of costly intergroup chases with the distribution of latrines.

The mate-guarding hypothesis proposed by Komers and Brotherton (1997) predicts that monogamous primates will occupy non-overlapping territories when females are distributed in small and discrete ranges, because males can defend them from other male competitors more easily.

Indri fits the model because groups cooperatively defend a small territory size; by doing this they defend their feeding resources, but also their mates and their progeny's survival. The expensive locomotion (vertical clinging and leaping) compared to indri body size (6.5 kg) favours the use of other territorial strategies such as advertising territory occupancy by loud chorus rather than patrolling on the boundary (Powzyk 1997). Pollock (1975) suggested that the loud song spreads up to 2 km from the singers in optimal conditions. The high detectability of the advertisement song (Maretti et al. 2010) can be instrumental in avoiding spatial overlap between territories.

Further, Pollock (1975) found that a group can locate and immediately reach the boundary in case of intrusion in its territory limits; however, indri presents the lowest encounter rate in comparison to the other 40 primates that display range defence (Cheney & Seyfarth 1987; Reichard & Sommer 1997; Nievergelt et al. 1998), and physical fights are very rare.

These data are also in line with the suggestion that indri males defend the border to defend females, and they can succeed in doing so because the territory size is relatively small. Further, they might rely on the advertisement songs to avoid unnecessary territorial displays. Advertisement songs potentially allow individuals to recognize the identity and spatial position of neighbouring groups (Giacoma et al. 2010; Baker-Médard et al. 2013; Gamba et al. 2016), thereby reducing the probability of energetically costly intergroup encounters and violent fights along the boundaries (see also Wich & Nunn 2002; Dallmann & Geissmann 2009; Terleph et al. 2015). Considering the energetic balance, the production of the 1–2-minute advertisement song represents an energetically less demanding form of territorial defence than the 1–2-hour

song emitted during encounters, physical fights or systematic border patrolling as described in chimpanzees (Krebs 1977; Morton 1986; McDonald 1989; Cowlishaw 1992; Watts & Mitani 2001; Powzyk & Mowry 2006).

Further support of the cost–benefit explanation of territoriality is given by the rarity of encounters, and by the modality more frequently adopted: most encounters were resolved with the emission of songs (Torti et al. 2013) and only in four cases were followed by physical fights. Studies on the sympatric species *Propithecus diademata* (Powzyk 1997), which lacks conspicuous singing activity, are in line with the “economic” interpretation of the song spacing function (“economics of defendability”; Mitani & Rodman 1979), because diademed sifakas defend their territories by extensive and energetically costly patrolling, scent marks and frequent intergroup fights.

A study on Verreaux's Sifaka reported an average territory size of 7.31 ha with an overlap between 36.5–63.7% (Benadi et al. 2008). In this species, the rate of encounters is six per month and 72% of cases reach aggression (Koch et al. 2016). In white-handed gibbons, another monogamous, territorial singing primate, the overlap between neighbouring territories is higher than in indri. Intergroup encounters not only are more frequent (0.8 encounters per day), but they more often involve physical rather than vocal interactions, without being necessarily aggressive (Bartlett 2003).

In indris, we found that once territorial boundaries have been set, neighbouring groups may not necessarily represent a threat to adjacent territory owners (Briefer et al. 2008), which can largely ignore and rarely challenge each other (Whitten 1982). At lower population density, as in Betampona (6.9–13.2 ind/km²), a larger territory size and a lower encounter rate have been reported, probably influenced by reduced pressure among neighbouring groups (Glessner & Britt 2005). The low overlap and encounter rate that we found, even at higher population density, underline the efficiency of the strategies that indri adopts to advertise and maintain territory exclusivity. In territorial, monogamous species, neighbour encounters can represent an opportunity to meet potential mates, as has been suggested for gibbons, *Hylobates lar* (Reichard & Sommer 1997), and common marmoset, *Callithrix jacchus* (Lazaro-Perea 2001).

We suppose that territorial behaviour in indri is related to the mate-guarding strategy and that the vocal behaviour plays a fundamental role in

regulating intergroup spacing dynamics. Additional studies about territory stability over time and space use with feeding resource availability will provide further data to quantify the cost–benefit balance of territorial behaviour in indri, still scarcely investigated using a quantitative approach.

Acknowledgements

This research was supported by Università degli Studi di Torino and the ACP Science and Technology Program of the ACP Group of States, with the financial assistance of the European Union, through the Projects BIRD (Biodiversity Integration and Rural Development; no. FED/2009/217077) and SCORE (Supporting Cooperation for Research and Education; Contract no. ACP RPR 118 # 36) and by grants from the Parco Natura Viva – Centro Tutela Specie Minacciate. We are grateful to Compagnia di San Paolo for co-financing the “Progetto 2008–10 Innovazione Laboratori didattici – Facoltà di Scienze MFN” which enabled the purchase of laboratory equipment used by VT, VS and GB during the field activities. We thank the Ministère de l’Environnement et des Forêts (MEF) and Madagascar National Parks for granting the research permits since 2004 (2004 (no. 190/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH) 2005 (no. 197/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH), 2006 (no. 172/06/MIN ENV.EF/SG/DGEF/DPB/SCBLF), 2007 (no. 02 20/07/MINENV.EF/SG/DGEF/DPSAP/SSE), 20 08 (no. 258/08/MEFT/SG/DGEF/DSAP/SSE), 20 09 (no. 243/09/MEF/SG/DGF/DCB.SAP/SLRSE), 2010 (no. 118/10/MEF/SG/DGF/DCB.SAP/SCB SE; no. 293/10/MEF/SG/DGF/DCB.SAP/SCB) and 2011 (no. 274/11/MEF/SG/DGF/DCB.SAP/SCB). We are grateful to GERP (Groupe d’Etudes et des Recherches sur les Primates) and to R. Dolch and the Mitsinjo Association for allowing us to collect data in the forests under their management. Finally, we thank Dr Cesare Avesani Zaborra and Dr Caterina Spiezio for helping us with the organization of the field station in Maromizaha. We thank Prof. Emilio Balletto for language proofing and manuscript revision. We are grateful to all the research and international guides, and to Lanto and Mamatin, for their help and logistical support. The contents of this document are the sole responsibility of the authors and can under no circumstances be regarded as reflecting the position of the European Union.

Funding

This work was supported by the ACP-EU Science and Technology Program [ACP RPR 118 # 36, no. FED/2009/217077].

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