Distribution and demography of white-faced tamarins *Leontocebus* spp. in Amazonian Ecuador – are they influenced by human activities?

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ABSTRACT – Understanding the effects of anthropogenic factors on the distribution and demography of the three tamarin species, *Leontocebus*, in Ecuador is key for their long-term conservation. In this study, I analyzed field data on the distribution and demography of the three species, obtained from 1989 through 2014, at 23 locations in the Ecuadorian Amazon. Comparing data on group size and density estimates for each species among habitats that differ in their degree of disturbance, I present a preliminary evaluation of the anthropogenic effects on species populations. The surveys confirm that *Leontocebus nigricollis graellsi* in Ecuador is restricted to the north bank of the Napo River, whereas *L. tripartitus* and *L. lagonotus* occur only in forests to the south of the Napo River. Data on the interviews with people in villages and with personnel of the Ministry of the Environment suggest the release of captive animals is a frequent practice that might explain confusing records of species sympatry. Higher population densities of *L. nigricollis graellsi* and *L. lagonotus* were found in the less disturbed forests, suggesting that habitat degradation and fragmentation are affecting their demography. Overall, these species are in need of more surveys in new Amazonian sites, genetic studies to assess areas of hybridization, and environmental education programs to eliminate wildlife traffic. Supported by CI/Primate Action Fund and USFQ grants.

Keywords: Callitrichidae; geographic range; group size; density, anthropogenic impact.

RESUMO – Distribuição e demografia dos saguis-de-cara-branca *Leontocebus* spp. na Amazônia Equatoriana – eles são influenciados pelas atividades humanas? Compreender os efeitos dos fatores antropogênicos sobre a distribuição e a população das três espécies de saguis *Leontocebus* no Equador é um elemento-chave para a sua conservação a longo prazo. Neste artigo, foram analisados dados de campo obtidos entre 1989 e 2014, em 23 localidades na Amazônia equatoriana, sobre a distribuição e a população dessas três espécies. Ao comparar o tamanho dos grupos e as estimativas de densidade populacional de cada espécie em *habitat* com diferenciados graus de alteração, apresentamos uma avaliação preliminar dos efeitos antropogênicos sobre as populações dessas espécies. Censos confirmam que, no Equador, *Leontocebus nigricollis graellsi* é restrita à margem norte do Rio Napo, enquanto *L. tripartitus* e *L. lagonotus* vivem nas florestas ao sul do Rio Napo. Entrevistas com moradores e funcionários locais do Ministério do Meio Ambiente sugerem que a soltura de animais provenientes de cativeiro é uma prática comum, o que poderia explicar os registros em simpatria dessas espécies. As maiores estimativas de densidade populacional para *L. nigricollis*

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graellsi e *L. lagonotus* foram encontradas nas florestas com menor grau de perturbação, sugerindo que a degradação e a fragmentação florestal afetam a demografia dessas espécies. Levantamentos populacionais em novas áreas de estudo, estudos genéticos para avaliar possíveis áreas de hibridação e programas de educação ambiental, visando eliminar o tráfico de animais silvestres, são necessários. Pesquisa patrocinada por doações da CI/Primate Action Fund e fundos da USFQ.

Palavras-chave: Callitrichidae; distribuição geográfica; tamanho do grupo; densidade; impacto antropogênico.

RESUMEN – Distribución y demografía de los chichicos de cara blanca *Leontocebus* spp. en la Amazonía ecuatoriana – ¿están siendo afectadas por actividades humanas? Entender los efectos de factores antropogénicos sobre la distribución y demografía de las tres especies de chichicos, *Leontocebus*, en Ecuador es clave para su conservación a largo plazo. En este artículo analicé datos de campo, obtenidos entre 1989 y 2014 en 23 localidades de la Amazonía ecuatoriana, sobre la distribución y demografía de estas tres especies. Al comparar el tamaño de los grupos y las estimaciones de densidad poblacional para cada especie en hábitats que difieren en el grado de alteración, presento una evaluación preliminar de los efectos antrópicos sobre las poblaciones de estas especies. Los censos confirman que en Ecuador, *Leontocebus nigricollis graellsi* está restringido al margen norte del río Napo, mientras que *L. tripartitus* y *L. lagonotus* habitan sólo en bosques al sur del río Napo. Entrevistas a gente de las comunidades locales y personal del Ministerio del Ambiente sugieren que la liberación de animales cautivos es una práctica frecuente que podría explicar los registros confusos de simpatría en estas especies. En *L. nigricollis graellsi* y *L. lagonotus* las densidades más altas fueron encontradas en los bosques menos disturbados. Esto sugiere que la degradación y fragmentación de los bosques están afectando a la demografía de estas especies. Se requieren más censos en nuevas áreas, estudios genéticos para evaluar zonas de hibridación potencial, y programas de educación ambiental para eliminar el tráfico de animales vivos. Investigación auspiciada por becas de CI/Primate Action Fund y USFQ.

Palabras clave: Callitrichidae; rango geográfico; tamaño de grupo; densidad; impacto antropogénico.

Introduction

Tamarin taxonomy has undergone important changes in recent years (Matauschek *et al.* 2011, Buckner *et al.* 2015). Based on a multi-locus phylogeny and a biogeographic analysis, Buckner and collaborators (2015) divided the genus *Saguinus* into two: *Leontocebus* with the small, white-mouthed tamarins, and *Saguinus* comprising the larger tamarins. Thus, the three Ecuadorian tamarin species, formerly in the genus *Saguinus*, are now recognized as species of *Leontocebus* Wagner, 1839 (Rylands *et al.* 2016). These three species are: Graells' black-mantled tamarin, *L. nigricollis graellsi* (Jiménez de la Espada 1870), the golden-mantled saddle-back tamarin, *L. tripartitus* (Milne-Edwards 1878), and the red-mantled saddle-back tamarin, *L. lagonotus* (Jiménez de la Espada 1870). The first two species, *L. nigricollis graellsi* and *L. tripartitus*, are classified as Vulnerable and *L. lagonotus* as Near Threatened in the *Red Book of Ecuadorian Mammals* due to the extent of their distribution and the high rates of deforestation and habitat degradation of the Ecuadorian Amazon (Mosandl *et al.* 2008, FAO 2010, Tirira 2011).

Leontocebus nigricollis graellsi and *L. tripartitus* have more restricted distributions (north and south of the Napo River, respectively), than *L. lagonotus*, which also occurs south of the Napo River (Rylands *et al.* 2011, Tirira 2011, de la Torre 2012). However, the exact boundaries of their distributions, especially of the two species that occur south of the Napo River, are not known. This lack of information poses a problem for designing and implementing effective actions to conserve these species. It is also unknown how human activities may be affecting the species demography. In this paper, I present data on the distribution of these three *Leontocebus* species obtained from 1989 through 2014 throughout their geographic range in Ecuador. In addition, I compare data on group size and population density among habitats that differ in their degree of anthropogenic disturbance to evaluate whether the demographics and distribution of these species are influenced by human activities.

Methods

One- to two-day surveys were carried out from 1989 through 2014 at 23 sites to confirm the presence or absence of the three tamarin species (Table 1, Figure 1). All surveys were carried out from 06h00 to 09h00 and from 16h00 to 18h00 in trails used by local people. Records of the species were based only in direct observations of wild tamarins. GPS coordinates from each of the observation sites were plotted on hydrographic, topographic and vegetation maps. Field surveys of the geographic range of these species were supplemented with bibliographic sources (*e.g.*, Albuja 1994, Rylands *et al.* 2011) and interviews with members of local communities as well as personnel of the Ecuadorian Ministry of the Environment. The potential boundaries for the distribution of each species were defined by a combination of field data, watersheds (Ayres and Clutton-Brock 1992), and relief.

Table 1 – Survey sites, ordered from North to South, years of observation and reference coordinates are presented (see Figure 1 for locations).

Site #	Locality	Year of observation	Latitude	Longitude
1	Putumayo River /south bank	2000	0°04'01"S	75°27'30"W
2	Güepi River	2000	0°07'23"S	75°30'19"W
3	Lagartococha River/Garzacocha	2005	0°28'07"S	75°20'08"W
4	Cuyabeno Reserve/Laguna Grande, Cuyabeno River	1989 - 1990	0°0'18"S	76°10'21"W
5	Lagartococha River/Imuya Lake	1997	0°36'06"S	75°14'03"W
6	San Francisco	2007	0°01'55"S	77°29'50"W
7	Lumbaqui	2008	0°03'16"S	77°20'24"W
8	Secoya territory of San Pablo de Katesiaya	2004-2005, 2009-2010	0°16'34"S	76°25'46"W
9	Secoya territory/Sehuaya	2009	0°18'02"S	76°16'44"W
10	Zancudococha	1997	0°36'02"S	75°28'57"W
11	Sacha Lodge Private Reserve	2002-2003	0°28'9S"S	76°27'59"W
12	Indillama community	1994, 2012	0°25'64"S	76°34'38"W
13	Jatun Sacha Reserve	2004	1°04'58"S	77°36'50"W
14	Selva Viva Private Reserve	2003-2004	1°03'28"S	77°31'25"W
15	Pompeya Sur-Río Iro road	1994, 2012-2014	0°27'40"S	76°35'35"W
16	Yasuní Research Station	1994	0°40'31"S	76°23'52"W
17	Yarina Reserve	2012	0°27'52"S	76°50'38"W
18	Tiputini Biodiversity Station – USFQ	2013	0°38'14"S	76°09'05"W
19	Nuevo Rocafuerte	2012	0°55'47"S	75°24'07"W
20	Tambococha – Yasuní National Park	2012	0°58'41"S	75°25'33"W
21	Pichincha/Yasuní National Park	2012	1°03'29"S	75°27'58"W
22	Yanacocha Private Reserve	2014	1°27'55"S	77°59'16"W
23	Omaere Ethnobotanic Park	2003	1°28'27"S	77°59'44"W

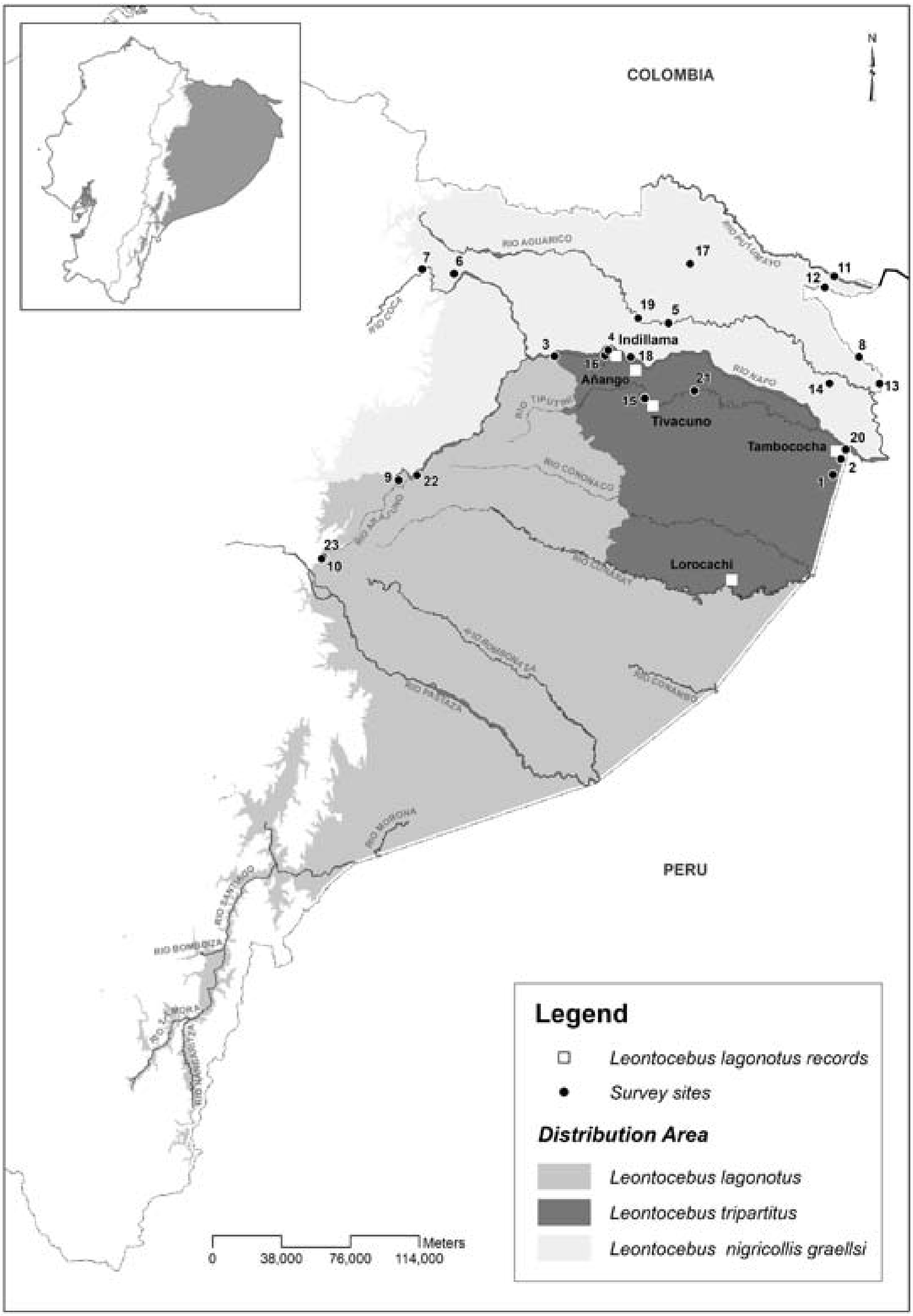

Figure 1 – Proposed distributions of the *Leontocebus* species in Ecuador. Observation/survey sites (sites are ordered from North to South): 1. Putumayo River /south bank, 2. Güepi River, 3. Lagartococha River/Garzacocha, 4. Cuyabeno Reserve/Laguna Grande, Cuyabeno River, 5. Lagartococha River/Imuya Lake, 6. San Francisco, 7. Lumbaqui, 8. Secoya territory of San Pablo de Katesiaya, 9. Secoya territory/Sehuaya, 10. Zancudococha, 11. Sacha Lodge Private Reserve, 12. Indillama community, 13. Jatun Sacha Reserve, 14. Selva Viva Private Reserve, 15. Pompeya Sur-Río Iro road, 16. Yasuni Research Station, 17. Yarina Reserve, 18. Tiputini Biodiversity Station – USFQ, 19. Nuevo Rocafuerte, 20. Tambococha – Yasuní National Park, 21. Pichincha/Yasuní National Park, 22. Yanacocha Private Reserve, 23. Omaere Ethnobotanic Park.

In order to assess the influence of anthropogenic disturbance on group size and population density, I studied wild groups of the three species in eight of the studied sites (Table 2). These eight sites comprised forests with different degrees of anthropogenic alteration. Forest characterization was carried out by estimating both the total area of primary *vs* secondary forest and the extent of forest fragmentation, based on the number and average area of the forest patches, using Landsat images of the sites from the years when the study was accomplished. Spatial analyses were validated with field observations and carried out with ArcGIS 10.1. Complementary data from interviews with local people and personal observations were also used to assess the hunting pressure in each site. Based on these criteria, the forests were classified as well preserved vs. moderately disturbed vs. severely disturbed (Table 2).

Table 2 – Study areas for each of the Leontocebus species.

Species	Site	Years of observation	Sampling days	Surveyed area (ha)	Forest conservation status
Leontocebus nigricollis graellsi	Cuyabeno Reserve/ Laguna Grande, Cuyabeno River	1989–1990	128	110	Well preserved forest, not affected by deforestation, fragmentation or hunting
	Sacha Lodge Private Reserve	2002-2003	42	100	Moderately disturbed forest. Regenerated area used for agriculture and selective logging 20 years ago. Hunting not allowed in the reserve
	Secoya territory of San Pablo de Katesiaya	2004-2005, 2009-2010	40, 42	100	Severely disturbed forest, highly fragmented, matrix of pasture, manioc and plantain cultures
L. tripartitus	Tiputini Biodiversity Station – USFQ	2013	30	100	Well preserved forest, not affected by deforestation, fragmentation or hunting
	Tambococha – Yasuní National Park	2012	6	50	Moderately disturbed forest, affected by selective logging and hunting 25 years ago
L. lagonotus	Selva Viva Private Reserve	2003-2004	30	50	Moderately disturbed forest Regenerated area used for agriculture and selective logging 15 years ago. Hunting not allowed in the reserve
	Yanacocha Private Reserve	2014	15	50	Severely disturbed forest surrounded by urban and suburban areas. Regenerated area used for agriculture and selective logging 10 years ago

Daily observations of tamarin groups in each site were carried out from 06h00 to 10h00 and from 15h00 to 18h00. Group size was recorded by counting all the animals in a group. Since all groups were observed for more than one day, repeated counts were used to record group size accurately. In order to assess whether group size was affected by forest conservation status (well preserved vs. moderately disturbed *vs.* severely disturbed), a one-way ANOVA was performed to compare the square root transformed group size among the three areas where *L. n. graellsi* was studied (well preserved vs. moderately vs. severely disturbed). In *L. tripartitus* (well preserve vs. moderately disturbed) and *L. lagonotus* (moderately disturbed vs. severely disturbed) unpaired t-tests were used.

To estimate population density (individuals/ha) for each of the species in each site, first the total number of individuals in a site was estimated by multiplying the total number of groups recorded by the maximum number of individuals in each group (if a group changed its size during the study period, the largest number was used for this estimation). Then, this estimated total number of individuals was divided by the sampling area. These calculations might overestimate density since some of the groups recorded at a site may occupy areas outside the sampling area (de la Torre *et al.* 1995a). However, by using the same criteria in all populations, comparisons among sites with different degrees of human alteration were possible. Spearman's rank-order correlations were carried out between the ranked conservation status of the areas (1: well preserved, 2: moderately disturbed, 3: severely disturbed) and the estimated population density. Since population densities of *L. tripartitus* were the same in the two study areas (see below), no correlation was calculated for this species.

Results

Species distribution

Leontocebus nigricollis graellsi, found only north of the Napo River, was recorded in the following locations (see Figure 1): Putumayo River/south bank (site 1), Güepi River (site 2), Lagartococha River/Garzacocha (site 3), Cuyabeno Reserve/Laguna Grande (site 4), Lagartococha River/Imuya Lake (site 5), Lumbaqui (site 6), San Francisco (site 7), Secoya territory/San Pablo (site 8), Secoya territory/Sehuaya (site 9), Zancudococha (site 10), and Sacha Lodge Private Reserve (site 11). The altitudinal range of these locations goes from 1100 masl (meters above sea level) in San Francisco in the west, to 200 masl in Lagartococha River in the east.

In all these locations, *L. nigricollis graellsi* was the only tamarin recorded. Interviews with members of the Secoya communities of San Pablo, Sehuaya, Aguas Blancas and Puerto Estrella, and of the Kichwa community of Zancudococha supported these findings. In two groups, one at Sacha Lodge Private Reserve and the other at Secoya territory/San Pablo, one adult individual from each group had a white vertical stripe, going from the middle of the eyebrows back to the nape, but maintained all the other morphological characteristics of *L. nigricollis graellsi*, with a dull olive-brown lower back, rump and thighs. Apparently, this white-fur variation occurs in other populations across the species range in Ecuador since individuals of this species with white stripes on the lower back have been observed by tourist guides in San Carlos (0°27'27"S, 76°53'40"W) and Limoncocha (0°23'55"S, 76°37'05"W) forests, in the north bank of the Napo River (R. Romero pers. comm.).

Leontocebus tripartitus and *L. lagonotus* were found only south of the Napo River. Groups of *L. tripartitus* were recorded in the following locations (see Figure 1): Indillama community (site 12), Pompeya Sur-Río Iro road (from the south bank of the Napo River to the south bank of Yasuní River, site 15), Yasuní Research Station (site 16), Yarina Reserve (site 17), Tiputini Biodiversity Station (site 18), Nuevo Rocafuerte (site 19), Tambococha-Yasuni National Park (site 20), and Pichincha/Yasuní National Park (site 21). The altitudinal range of these locations goes from 280 masl in Yarina Reserve in the west, to 190 masl in Tambococha in the east. Individuals within and among populations varied in the intensity of their orange fur on the lower back and rump.

Groups of *L. lagonotus* were recorded in the following locations (see Figure 1): Jatun Sacha Reserve (site 13), Selva Viva Private Reserve (site 14), Yanacocha Private Reserve (site 22), and Omaere Ethnobotanic Park (site 23). Interviews with members of the Waorani community of

Quehueri'ono (1°0'09"S, 77°08'19"W) confirmed the presence of the species along the Shiripuno River. The altitudinal range of these locations is from 1000 masl in Omaere and Yanacocha reserves in the west, to 260 masl along the Shiripuno River in the east. Individuals were variable in the intensity of the reddish color of their mantle, arms and legs within and among populations. One captive individual in the area of Puyo (Pastaza Province) had white mantle and arms; however, this color changed to the species' typical reddish brown four months after a change in diet (J. Flores, pers. comm.).

Group size and population density

Mean group size of *L. nigricollis graellsi* ranged from 6.3 ± 1.2 in Sacha Lodge to 5.5 ± 1.9 in Cuyabeno (Table 3). Differences in group size among populations were not significant. Ten groups were recorded using totally or partially the 110-ha study area in Cuyabeno, the least disturbed forest; six groups were recorded in 100 ha around Sacha Lodge, with moderate forest disturbance. Only three groups of the species were recorded in 100 ha of the severely disturbed forests of San Pablo. Estimated population densities ranged from 50 ind/km^2 in Cuyabeno to 17 ind/km^2 in San Pablo. In San Pablo, the population density of this species decreased by about 50% in a 5- year period (17 ind/km^2 in 2004-2005 vs 7 ind/km^2 in 2009-2010).

Table 3 – Mean group size (± SD) and estimated population density of the Ecuadorian *Leontocebus* species in study areas that differed in the degree of habitat disturbance. In San Pablo, density estimates are presented for two periods [1]: 2004-2005, [2]: 2009-2010.

Site	Forest conservation status	Area sampled (ha)	No. of groups	Mean group size ± SD	Pop. density (ind/km^2)
Leontocebus nigricollis graellsi					
Cuyabeno Reserve	Well preserved	110	10	5.50 ± 1.9	50
Sacha Lodge Reserve	Moderately disturbed	100	6	6.33 ± 1.2	38
San Pablo / Secoya territory	Severely disturbed	100	3	5.67 ± 1.2	17 [1], 7 [2]
Leontocebus tripartitus					
Tambococha/Yasuní National Park	Well preserved – some intervention	50	2	5.0 ± 1.4	20
Tiputini Biodiversity Station / Yasuní Biosphere Reserve	Well preserved	100	4	5.0 ± 0.8	20
Leontocebus lagonotus					
Selva Viva Reserve	Moderately disturbed	50	2	7.5 ± 0.7	30
Yanacocha Reserve	Severely disturbed	50	2	6.5 ± 3.5	26

Mean group size in *L. tripartitus* did not differ significantly between the two study areas (Table 3). Four groups were recorded in 100 ha in Tiputini, the well preserved forest, whereas two groups were recorded in about 50 ha in the moderately disturbed forest of Tambococha. Estimated population densities were 20 ind/km^2 in both sites.

Mean group size in *L. lagonotus* was larger in Selva Viva, the moderately disturbed forest, than at Yanacocha, the severely disturbed forest, although the difference was not significant (Table 3). Two groups were recorded in each area. Estimated population densities were 30 ind/km^2 in Selva Viva and 26 ind/km^2 in Yanacocha.

Spearman's correlations of the conservation status of forests and the population density were not significant due to small sample sizes. In *L. nigricollis graellsi*, the correlation coefficient was strong and negative (r = -1) as in *L. lagonotus*. These negative correlation coefficients suggest that population densities of *Leontocebus* in Ecuador may be adversely affected by the degree of disturbance of the forest.

Discussion

These results complement previous information about the distributions of the three species of *Leontocebus* in Ecuador (Rylands *et al.* 2011). New limits of the distributions of *L. lagonotus* and *L. tripartitus* are presented, extending to the west, in about 20 km, the previously reported distribution of *L. tripartitus* in the southern bank of the Napo River (Rylands *et al.* 2011). The results also suggest that the current areas of distribution of the *Leontocebus* species in Ecuador are influenced by human activities. I will discuss first how my results contribute to the current knowledge of the species' distributions. Then, I will analyze the anthropogenic effects on the species' demography.

Based on these field surveys and interviews, it is evident that the distribution of *L. nigricollis graellsi* in Ecuador is restricted to the north of the Napo River and to the south of the Putumayo River, along the Andean slopes, to an altitude of approximately 1200 masl, its western boundary. To the east, the distribution of this species reaches the Ecuador-Peru border (Figure 1). *L. tripartitus* appears to be restricted to the south of the Napo River and the north of the Curaray River. Its western boundary may be the confluence of the Shiripuno and Cononaco rivers, north to the south bank of the Napo River in the area of Yarina (approximately 15 km south-east of the confluence of the Coca and Napo rivers). In the south, its western boundary may be the mouths of the Tigüino and Cunchiyacu rivers, south to the north bank of the Curaray River (Figure 1). The distribution of *L. lagonotus* in Ecuador is restricted to the southern bank of the Napo River, along the Andean slopes, to an altitude of approximately 1000 masl, its western boundary. The eastern boundary seems to vary with latitude. In the north, close to the Napo River, the limit may be the confluence of the Shiripuno and Cononaco rivers, whereas from the south bank of the Curaray River, the eastern limits expand to the Ecuador-Peru border (Figure 1). The presence of *L. lagonotus* along the south bank of the Curaray River in Peru was confirmed by Heymann *et al.* (2002).

Previous maps of the *L. tripartitus* distribution in Ecuador (*e.g.*, Rylands *et al.* 2011) placed this species about 20 km to the east, south of the Indillama River (a southern tributary of the Napo River in that area). These maps were based on observations of *L. lagonotus* in an area north of the Indillama River, close to the Pompeya Sur-Río Iro road, reported in 1994. This previous geographic range comprised a ~6-Km-wide fringe between the Napo and the Indillama rivers as occupied by *L. lagonotus*. Recent and more detailed observations of *L. tripartitus* in this area suggest that this might be a region of sympatry between the two species. However, past observations of *L. lagonotus* might also have been of captive animals released by people, considering that records of *L. lagonotus* in that area have been sporadic compared to those of *L. tripartitus*.

Live capture and trade of tamarins are common in Amazonian communities in Ecuador, as reported in interviews with members of local communities (Kichwa, Waorani, Secoya, Shuar and colonos). Such practice might have eventually led to introductions of individuals of a species into areas where it does not occur naturally. These introductions may have occurred for many years and may explain some records of *L. lagonotus* in areas where *L. tripartitus* has been regularly recorded (Figure 1):

- brief (5–10 min) observations of *L. lagonotus* recorded by the author in 1994 in the land of the Kichwa community of Indillama, close to the Pompeya Sur-Río Iro road (Rylands *et al.* 2011).
- a report of the presence of one individual of *L. lagonotus* in Lorocachi (1°36'18"S, 75°58'40"W), at the north bank of the Curaray River in 2011 by personnel from the Ecuadorian Ministry of the Environment (E. García pers. comm.).
- Albuja's (1994) reports of individuals of *L. lagonotus* along the Tambococha River (0°54'12"S, 75°35'58"W) and at the mouth of the Tivacuno River, where it drains into the Tiputini River (0°42'39"S, 76°21'22"W).

Erroneous re-introductions of tamarins might also occur due to errors in species identification or limited knowledge about species' natural distributions by personnel of the Ministry of the Environment, who oversee the release of confiscated tamarins into the wild. Personnel from the Ministry of the Environment reported to the author, for example, a release of one individual of *L. lagonotus* in the Kichwa community of Añango in 2012 (E. García pers. comm.), a natural area of *L. tripartitus*.

Hybridization might be occurring if two species of *Leontocebus* are sharing the same area, either naturally or by human influences. Hybridization among tamarin species due to human interference was reported by Hershkovitz (1977) and was also observed by the author, between *L. nigricollis graellsi* and *L. lagonotus*, in a rescue center in Tena (Napo Province) in 2012. However, the fertility of the offspring could not be confirmed. No observations of possible hybrids between *L. lagonotus* and *L. tripartitus* have been reported yet, but their occurrence is not unlikely if few individuals of one species are introduced in the area of the other. Provided that this is the case, the traffic of live tamarins might be affecting not only the geographic distribution of the species but also their genetic diversity.

The impacts of human activities on the geographic distribution of the Ecuadorian tamarins may also be occurring through changes in their demographics (*e.g.*, births, deaths, dispersal rates). Forest degradation and fragmentation might reduce population size and affect the dispersal of individuals increasing the probability of local extinctions (Pulliam 1988, Primack and Miao 1992). The reported differences in estimates of population density among forests with different degrees of alteration, found in *L. nigricollis graellsi* and *L. lagonotus*, suggest that habitat degradation and fragmentation are indeed affecting the population densities of the tamarins. In both species, higher densities were found in the less disturbed forests. The lowest density estimates were found in the forests of San Pablo for *L. nigricollis graellsi*, and Yanacocha for *L. lagonotus*, both characterized by severe fragmentation. The reported reduction in density of *L. n. graellsi* in San Pablo over the years coincides with an increase of deforestation and forest fragmentation in that area (de la Torre *et al.* 2013), indicating the impact that forest degradation, fragmentation, and other human activities might have on the specie's demographics.

Estimates of population density for *L. tripartitus* were lower than those for the other species and did not differ between study areas. Although the area of Tambococha historically suffered from human activities more than Tiputini, this result suggests that the current conservation status of both forests is similar (or that the species in both sites is at its upper limit with a density of 20 ind/km^2). Due to the way in which the population densities were estimated (over-estimated), it is not possible to compare the absolute values with the results of other studies (*e.g.,* Rosin and Swamy 2013). However, it is possible to analyze whether the causes of the differences in population densities (among areas or species) provided by other researchers also explain the patterns reported in this study. Some authors have found evidence that small primates such as *Leontocebus* and *Saguinus* have higher densities in areas where larger primates have been extirpated (Goldizen 1987, Rosin and Swamy 2013). The areas of Tiputini and Tambococha are inhabited by other nine primate species, all of which, with the exception of the pygmy marmoset *Cebuella pygmaea*, are larger than *L. tripartitus* (see Marsh 2004). The reported low densities of *L. tripartitus* in both areas could therefore be related to the presence of medium-sized (*e.g.*, the Marañón white-fronted capuchin *Cebus yuracus*) and large (*e.g.*, the white-bellied spider monkey *Ateles belzebuth*) primates in these forests. It is difficult, however, to relate the high estimates of population density of *L. nigricollis graellsi* in Cuyabeno with a potential compensatory response to the absence of large primates, since nine other primate species occur there and eight of them are larger than the tamarins (de la Torre *et al.* 1995b). On the other hand, in San Pablo, where I recorded the lowest density for *L. nigricollis graellsi*, there are only two other primates (*C. pygmaea* and the red-crowned titi *Callicebus discolor*), neither of which outcompete *Leontocebus* at fruiting trees (pers. obs.). These results suggest that competition with larger primates is only one of a complex set of factors affecting the population density and distribution of *Leontocebus*, and that deforestation and forest fragmentation may be important determinants of demographic rates. More specific studies of the factors affecting population dynamics of these species are essential for implementing effective conservation actions.

More surveys are needed in the forests south of the Napo River to know in more detail the boundaries of the distributions of *L. tripartitus* and *L. lagonotus*, and to confirm possible areas of sympatry. The forests along the Indillama, Shiripuno, Cononaco, Tiputini, Tigüino, Cunchiyacu and Curaray rivers should be studied to obtain more exact maps of the geographic distributions of Ecuador's primates, and to better understand the current conservation status of their populations.

Released individuals of any of the species should be followed and periodically monitored to evaluate the impacts of their reintroductions. Such studies are more feasible when reintroductions are carried out by personnel of the Ministry of the Environment. The relevant ministry personnel need better training in *Leontocebus* taxonomy and distribution to reduce the problems that have been detected in previous reintroductions. Genetic studies to assess areas of hybridization and to reconfirm the *Leontocebus* species in Ecuador are important too. Environmental education campaigns to reduce, and eventually eliminate, wildlife traffic should be continued and reinforced. Such campaigns should focus not only on local communities (to prevent more erroneous reintroductions of tamarins) but on other sectors of the society, which also participate in this pernicious activity that is threatening Ecuadorian primates in ways that have not yet been quantified or understood deeply.

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