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Articles

SYMPATRIC DISTRIBUTION OF TWO SPECIES OF *ALOUATTA* (*A. SENICULUS* AND *A. PALLIATA*: PRIMATES) IN CHOCÓ, COLOMBIA

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Abstract

We studied a zone of sympatry between *Alouatta seniculus* and *Alouatta palliata* on the left bank of the Atrato River (Chocó). We located 110 groups of *Alouatta,* consisting of 81 groups of *A. palliata* and 29 groups of *A. seniculus*, recorded between 12 – 300 m a.s.l. *Alouatta seniculus* was associated principally with *arracachal* and *panganal* vegetation of alluvial soils alongside the Atrato River below 50 m altitude, and *A. palliata* was associated with upland vegetation of gallery forest, primary forest and secondary forest (20-300 m a.s.l.). The average number of animals per group of *A. seniculus* was 5.59 (range 2-7 individuals) while the average for *A. palliata* was 6.76 (range 2-18 individuals). No phenotypic evidence of hybridization was detected in contrast to other studies of hybridization of *Alouatta*. The condition of many of the forests in this study suggests the necessity of a conservation program in order to protect this unique zone of sympatry between the two species.

Keywords: *Alouatta seniculus*, *Alouatta palliata*, sympatry, Chocó, Colombia, primates

Resumen

Se estudió una zona de simpatría entre *Alouatta seniculus* y *Alouatta palliata* en la margen izquierda del río Atrato (Chocó). La distribución de ambas especies se determinó mediante observaciones directas y encuestas. Los árboles utilizados fueron identificados, la estructura y número de individuos en cada grupo determinado, la ubicación registrado con GPS y los datos fueron analizados con SIG para determinar posibles factores ecológicos y geográficos que limitan la presencia de las dos especies. Se observaron 110 grupos de *Alouatta* consistiendo en 81 grupos de *A. palliata* y 29 grupos de *A. seniculus* diferentes, a alturas que varían entre 12 y 400 msnm. *Alouatta seniculus* está asociada principalmente a vegetación de tierras aluviales por debajo de los 50 msnm y *Alouatta palliata* a tierras altas. El promedio del tamaño de los grupos de *Alouatta seniculus* fue de 5.59 animales (rango 2-7 individuos) y el de *A. palliata* de 6.76 (rango 2-18 individuos). No se detectó evidencia fenotípica de hibridización como se ha reportado en otros estudios de simpatría de *Alouatta*. El tipo de vegetación mayormente utilizado por *A. seniculus* fue arracachal y panganal de los bajos, y principalmente al lado del río Atrato, mientras que *A. palliata* utilizaba bosque de galería, bosque primario, y bosque secundario y rastrojo. La condición de muchos de los bosques en este estudio sugiere la urgente necesidad de un programa de conservación para proteger esta zona única de simpatría entre las dos especies.

Palabras clave: *Alouatta seniculus*, *Alouatta palliata*, simpatría, Colombia, primates

Introduction

Alouatta is the most wide-spread Neotropical primate genus, distributed from southern Mexico to northern Argentina (Milton, 1980; Crockett, 1998). In Colombia two species are found that are generally allopatric, though there are poorly defined historic records and some recent observations that suggest a large sympatric zone between *Alouatta palliata* and *A. seniculus* for northern Colombia extending from the left banks of the Peye and Atrato in the Chocó department to the region around Cartagena, south to the río Sinú (Fig. 1). Whether *A. palliata* was at all common in northern Colombia east of the Atrato River can no longer be said; it is now very scarce in the region, perhaps having been largely displaced by *A. seniculus* which has a high tolerance for anthropogenic disturbances (Defler, 2012; Eisenberg, 1979). Three of the 14 recognized *Alouatta* species are known to have allopatric distributions with other *Alouatta* species (Crockett and Eisenberg, 1987). Small sympatric overlaps are known for *Alouatta pigra* and *A. palliata* in Central America (Horwich and Johnson, 1986), *A. palliata* and *A. seniculus* in Colombia (Hernández and Cooper, 1976) and *A. caraya* and *A. fusca* in northeast Argentina (Crockett, 1998).

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This study was designed to describe and characterize the area of sympatric overlap between *A. palliata* and *A. seniculus* from a zone on the left bank of the Atrato River in the Darien, Colombia, and to search for phenotypical evidence of possible hybridization. We attempted to identify ecological factors characteristic of these species that could affect their distribution along the lower Atrato River. *Alouatta seniculus* persists at least sympatrically with *A. palliata* until the latitude of Quibdó (5°42′N) and, on the left bank of the lower Atrato river, *A. palliata* is present in the same region but on generally higher ground.

Methods

Study Area

The Colombian Darién in northwestern Colombia is part of the Chocó biogeographic region, recognized for its strategic position as a bridge between Central and South America. The region comprises the Panamanian province of Darién and the northern Chocó of Colombia and includes a forested low mountainous frontier between Panamá and Colombia as well as extensive lowland swamplands on both sides of the Atrato River. The climate of the region studied is generally drier than other parts of the Chocó to the south and has a unimodal annual precipitation between 1,900-3,100 mm, contrasting with the high precipitation of the central and southern portions of the department where the highest precipitations for any rain forest have been reported (13,300 mm in Lloró, south of Quibdó). Annual temperatures in the north are also higher at around 24° C in the lowlands, compared to further south (Rangel-Ch. and Arellano-P., 2004).

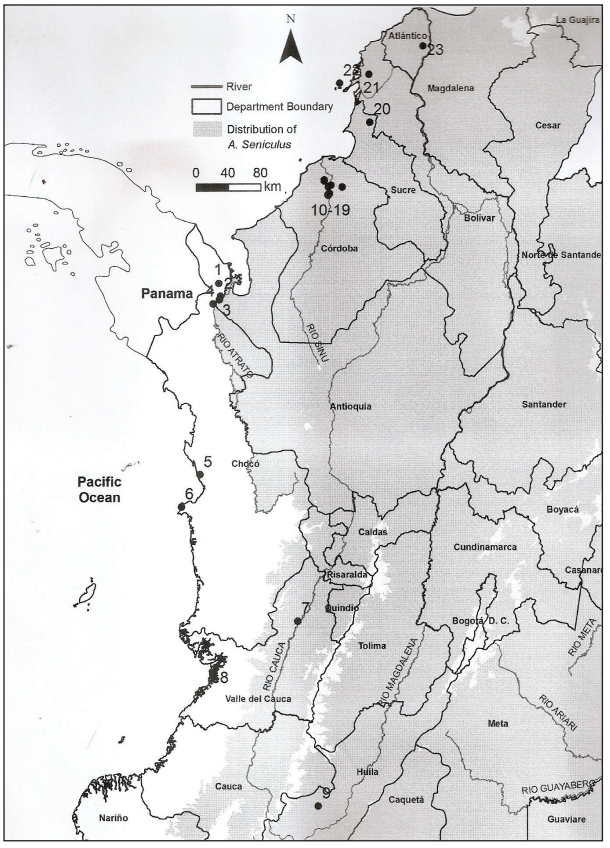


Figure. 1. Sympatry between *Alouatta palliata* (no. 2-4, 10-23) with *A. seniculus*. Numbers 10-20 are recent observations of biologists. Number 22 is an introduced island colony formed by animals introduced from the mainland (around no. 20) while 21 and 23 are historical records of past biologists.

Topography is varied from a wide belt of wetlands along the Atrato river at near sea level to hills and low mountains, that gradually increase in height towards the Panama border, becoming the low mountains of the Serranía del Darien, with average heights of only 500 m but a maximum height of 1,875 m for the Cerro Tacarcuna. Originally the entire region was covered in thick forest that could be classified as bh-T in the Holdridge life-zone system (Holdridge, 1967), but currently the region is in rapid conversion of the natural vegetation to an anthropogenic landscape (Rangel-Ch., 2004a). Current forest cover in the study area up to the boundary of Los Katios National Park is limited to fragments of primary forest and secondary forest representing distinct floristic communities. The forest fragments are generally surrounded by pasturelands used for cattle as well as cultigens (corn, yams, manioc, rice, plantains and bananas, sugar cane and some coca leaf) and tree plantations (particularly of cativo *Prioria copaifera*, ceder *Guarea aligero* and roble *Tabebuia rosea*). The principal economic activities in the zone are cattle ranching and small scale lumbering.

The study area includes the municipalities of Acandí (8°32' 00"N, 77°14'00"W) and Unguía (8°01'00"N, 77°04'07"W) [Colombian municipalities are similar to counties in the United States and include several towns and much countryside]. We selected ten localities because of confirmed presence of howlers and their locations, permitting reasonable access with manageable logistics. These localities were as follow: La Playona (Acandí), Balboa, Titumate, San Francisco, Tanela, Santa María la Nueva, Gilgal, Unguía and Los Katios National Park (Unguia). The particular characteristics of these localities are listed in Table 1. Data collection took place during the dry season between November, 2009 and February, 2010 (Table 1). The region has six sympatric species of primates; *Alouatta palliata, Alouatta seniculus, Ateles geoffroyi rufiventris* (=*Ateles fusciceps rufiventris*), *Cebus capucinus, Saguinus geoffroyi* and *Aotus zonalis,* but *Ateles geoffroyi* is becoming increasingly scarce due to hunting and habitat loss (Defler, in press-b).

Evaluating the species distribution

We used two methods to evaluate the distribution of the two species of *Alouatta*: unstructured interviews with local people and daily searches along paths and rivers (Pinto and Rylands, 1997; Iwanaga and Ferrari, 2002). The interviews consisted of questions about where groups had been seen, the color of their pelage and the type of vocalization. We also asked about hunting activities, the occupation of the interviewee and their time of residence in the area. People interviewed were principally subsistence hunters, small

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farmers, park guards and farm owners. Observations were made on foot and from boat. For each locality we noted GPS coordinates, number of individual primates observed, age-class, sex, pelage phenotype, height from ground when first observed, altitude over sea level, and the forest type. Individuals were classified as adults, subadults, juveniles and infants (Defler, 1981). We analyzed the coordinates of our observations using the program ArcGIS, version 9.3 (2008) in order to map them.

Forest habitat structure was classified and sketched by topography (hilly, hill top, sides of hills, lowland and swampy), forest type (primary, secondary, re-growth, special types of forest) and altitude above sea level. Vegetation structure was analyzed measuring DBH (diameter at breast height), tree height, and the identification of tree species. We measured tree height and DBH only from trees where the groups were first seen.

Results

We completed 85 interviews and obtained 132 locations for *Alouatta* groups. We were able to locate 110 groups at these locations. The 110 groups totaled 672 individual howler monkeys of which 29 groups were *A. seniculus* and 89 groups were *A. palliata*.

Alouatta seniculus

For *A. seniculus* we found the 27 observed groups of the species in five different localities, confirming the presence of the species in four forest types varying in altitude from 7- 35 m a.s.l. (average = 19.3 m). Their distribution was restricted to floodable river plains and swampy lowlands. Eighteen of the 27 groups were seen on the left bank of the Atrato river in *panganal* (*Raphia taedigera*) associations in Katios National Park (Fig. 2).

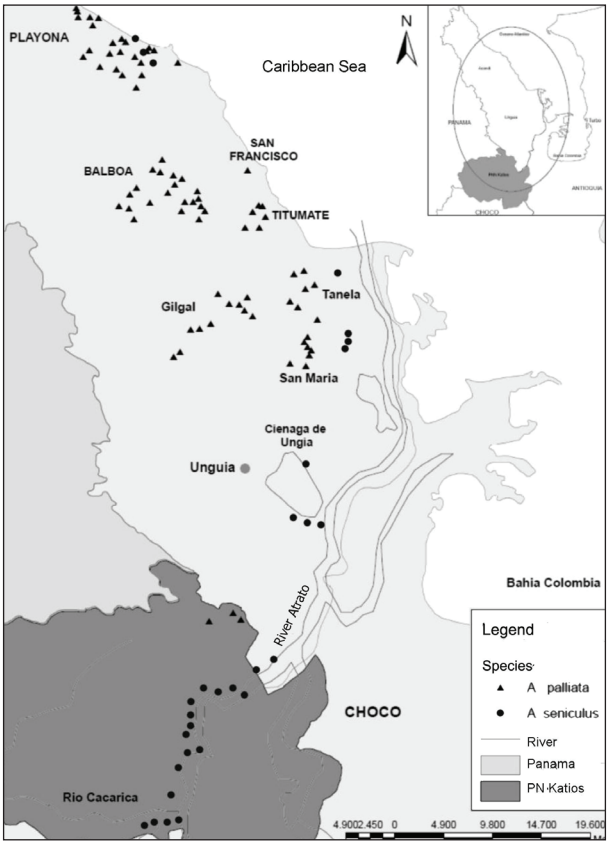


Figure 2. Distribution of howler groups in the Chocó Darien

Table 1. Sampled localities and condition of forest.

Site		Structure of Habitat	Selective Cutting		Hunting
PLAYONA		High forest and secondary fragmented vegetation surrounded by pasture	Medium/High		Very Low
BALBOA		Fragmented high forest and secondary vegetation with a mosaic of pastureland and cropland.	High During Study		Medium/High
TANELA		Very fragmented high forest surrounded by grasslands and cropland. Panganal Association is highly intervened.	Low at the present time.		Low
TITUMATE		High continuous forest surrounded by grassland and [oil] palm plantations.	Medium		Low
SAN FRANCISCO		Secondary growth surrounded by grasslands and tree plantations.	Medium		Low
SANTA MARIA		Secondary growth surrounded by grasslands and tree plantations.	Medium		Low
GILGAL		High forest, fragmented vegetation surrounded by grasslands and kitechen gardens.	High		High
UNGIA		Highly fragmented secondary vegetation surrounded by grasslands and conserved panganales.	Medium		Medium/High
PNN KATIOS		Continuous high forest and primary vegetation and conserved secondary vegetation, buffer zone wo cattle pastures.	Low		Low

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The *A. seniculus* groups had an average of 5.59 +/- 2.08 (range 2-12 individuals) (Table 2). Two groups contained 11 and 12 individuals. The groups were made up of 1 or 2 adult males, 1-3 adult females and 1-3 subadults; the number of infants varied generally from 0-5. We observed two solitary adult males. The ratio of male adults to female adults was 1:1.1 and the ratio of adult females to immature (infant + juvenile) animals was 1:1.3. Pelage color was generally totally red-orange (Burnt Sienna to Mahogany Red or Chestnut according to Hershkovitz, 1949), although in some individuals there was some blackish coloring in the pelage that could not be closely observed due to the shyness of this species. Dark patches would suggest genetic introgression from *A. palliata*. We observed *A. seniculus* 55.2% of the time atop palm trees at an average height of only 12.5 m. Middle parts of the low forest at about 9.2 m were used about 44.8% of the time.

Alouatta palliata

We observed *A. palliata* in nine localities, confirming the presence of this species in five types of forest. The altitude of these groups fell between 12– 400 m a.s.l. (average 94 m). They were principally observed in gallery forests and in old growth of secondary forest. The structure and composition of 76 groups of this species averaged 6.76 animals per group (range 2-18 individuals; DS: 3.6) (Table 3). Two groups had between 17 and 18 individuals. Groups usually had 1-3 adult males, 1-4 adult females, 1-3 subadults and from 0-3 immature animals for the 76 groups. The ratio of adult males to adult females was 1:1.5 and the ratio of adult females to immature animals was 1:0.99.

Usually the pelage of this species was totally black, although occasionally there were individuals with patches of brown on

Table 2. Age-sex composition for 29 groups of *Alouatta seniculus* in the Darien region of the Colombian Chocó.

Grupo	♂A	♀A	♂S	♀S	J♂	J♀	I	Undet.	Total Ind	Altitude (m)
P12	1	3	1	1	1				7	7
P20	1	2			2				5	20
TA7	1	2			1			3	7	3
SM4	1	1			1		1	1	5	16
SM5	1	1			1				3	13
SM6	1	1		2				1	5	18
U1	1		1	1				1	4	10
U2	1	1	1	1				1	5	10
U4	1	1	1	1				1	5	10
PK1	2	1			1			1	5	18
PK2	1	2	1			1			5	27
PK3	1	1		2	1		1		6	31
PK4	1	1			1	2			5	30
PK5	2	1							3	32
PK6	2	1	3	2		2	1	1	12	22
PK7	2	2	1			1		1	7	25
PK8	1	2	2		1				6	25
PK9			2					1	3	20
PK10	1		1	1				4	7	18
PK11	1	1	2					1	5	26
PK12	1	3			1	1			6	22
PK13	2	1	3	2	2		1		11	30
PK14	1	2			2				5	23
PK15			2	1					3	27
PK16	1	1					1	3	6	27
PK17	2	2			1				5	29
PK18	1	2	1	1					3	20
TOTAL	31	35	22	15	16	7	5	20	151	
Average	1.15	1.30	0.81	0.56	0.59	0.26	0.19		5.59	

A: adult, S: subadult, J: juvenil, I: infant, und

A: adult, S: subadult, J: juvenil, I: infante, Undet.: undetermined sex

P= PLAYONA, TA= TANELA, SM= SANTA MARIA, U= UNGUIA, PK= PARQUE

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Table 3. Composition of 76 Groups of *A. palliata* in the Darien region.

Group	♂*A*	♀*A*	♂*S*	♀*S*	♂*J*	♀*J*	*I*	Undet.	Total	Altitude (m)
P1	2	1			1				4	21
P3	1	1	1		1	1			5	19
P4	1	2	2	1	4		2		12	23
P5	2	1	1		1	1			6	36
P6	1	2							3	22
P7	1	2	4	4	2	3	1		17	25
P8	2	1	1	1			1		6	26
P9	2	4	1		3	4			14	24
P10	1	1							2	26
P11	3	4	3		4	2	2		18	30
P14	2	3	1		1	2			9	16
P16	1	2	3		1		2		9	25
P17	1	3	3			1	3		11	36
P18	1		1					1	3	30
P22	2		2	1			2		7	28
P23	2	3			2	1		1	9	34
P24	2	2							4	22
P25	1	2	1		1				5	29
P26	2	4			3	1			10	26
P27			2			1			3	17
B1	2	2	2			1	1		8	108
B2	2	3		2	1	1			9	102
B3	1	2	2		1	1			7	122
B4	2	2	1		1	3	2		11	110
B5	2	3	1		3	4	2		15	128
B6	1	1	2				1		5	109
B7	3	3	1			1	1		9	81
B8		1	1						2	156
B9	1	1	1	1		1			5	152
B10	2	3	1		2			1	9	167
B11	1	1	1						3	145
B12	2	4	3		1	1			11	163
B13	2	1			2	2			7	80
B14	2	1							3	83
B15	1	1	2						4	102
B17	1	2				2		1	6	110
B18	2	4			1	1			8	102
B19	1	1		1					3	146
B20	1	1							2	80
B21	2	4	1	1	2	1		1	12	114
SF	1	3	2		2	1			9	14
TA1	1	1	2			2			6	27
TA2	1	2	3	1	1				8	16
TA3	2	3			1			1	7	12
TA4	1		1	1					3	22

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Group	♂*A*	♀*A*	♂*S*	♀*S*	♂*J*	♀*J*	*I*	Undet.	Total	Altitude (m)
TA5	1	1							2	15
TA6	2	3			2	1			8	12
TA8		1	1						2	23
SM1	1			1				1	3	28
SM2	1	1			2	1	1		6	25
SM3	2	1							3	22
SM7	1	1							2	22
SM8	1	2	1		1				5	26
SM9	2	1							3	30
SM10	3	4			2				9	36
G1	1	2		1	1				5	209
G2	2	3	1		2			2	10	301
G3	3	1		1	1				6	322
G4	1	1							2	298
G5	2	2	1						5	298
G6	2	2	1		1	1		2	9	301
G7	1	1							2	245
G8	2	4	1		1				8	322
G9	1		1	1		1		1	5	136
G10	2	1			1				4	136
G11	2	4	1	1	2	1		2	13	79
PK1	2	3	2					1	8	19
PK2	3	1			1			2	7	35
PK3	3	2	1	1	1			1	9	31
T1	2	1			1	1			5	222
T2	1	1							2	191
T3	1	1	1		1	2	1		7	179
T4	2	1	1	1		2		1	8	100
T5	2	3			1				6	183
T6	1	2	2		3	2		1	11	169
T7	2	3	1		3	1			10	165
TOTAL	119	142	69	21	69	52	22	20	514	
Average	1.57	1.87	0.91	0.28	0.91	0.68	0.29		6.76	

A: adult, S: subadult, J: juvenile, I: infant, undet.: undetermined
ABREVIATIONS: P= PLAYONA, B= BALBOA, SF= SAN FRANCISCO, TA= TANELA, SM= SANTA MARIA, G= GILGAL, PK= PARQUE NACIONAL NATURAL LOS KATIOS, T= TITUMATE

the flanks and the dorsal area. One male adult had whitish coloration in the mesial part of the tail. There was no pelage evidence of hybridization with *A. seniculus* on these animals. We observed a total of five solitary animals, three of which were males, one was a solitary female and one was a solitary subadult sex unknown. The solitary subadult *A. palliata* was heavily infested by bot flies (*Alouattamyia baeri*?). *A. palliata* was seen 77.8% of time at canopy height of 22.7 +/- 5.0 m while the undergrowth was used only 22.2% of the time with an average height of 9.5 m +/- 3.3 m.

Forests habitat structure

Generally *A. palliata* and *A. seniculus* were associated with different types of habitat. The wetlands of Darién are dominated by plant communities like the *panganales*, *arracachales* and *cativales* (very impacted due to lumbering of the tall *cativo* tree [*Prioria copaifera*, Rangel-Ch, 2004a]) that are found along edges and dikes of the Atrato river, sometimes at the base of hills and terraces. P*anganales* are dominated by the pangana palm (*Raphia taedigera*), the *suerdo* (*Ficus dendrosida*, Cecropiaceae) and the *chachafruto*

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(*Erythrina fusca,* Fabaceae). In the medium stratum *cativo* (*Prioria copaifera*, Caesalpineaceae [an endangered tree species or EN in the IUCN system for Colombia], *yarumo* (*Cecropia* sp.) and *guamo* (*Inga* spp., Mimosaceae) are common. This type of forest is the most important for *Alouatta seniculus* and *Cebus capucinus* in the Darien region. Nevertheless it is one of the most transformed associations because of extraction of woody species and the opening of canals to drain flooded areas for use as pasture land.

Arracachales dominated by the widely distributed arracacho (*Montrichardia arborescens*, Araceae) is the principal association on the flood plain of the Atrato river. The *arracacho* (*Montrichardia arborescens* reaches 10-15 species per square meter with an average height of only 2 m (Plan de Manejo Katios, 2007). Arracachos grow in association with other dominant species such as *Blechnum serrulatum, Acostichum aureum, Scleria secans, Scleria melaceuca* and species of *Thelytpteris* and *Panicum* (Rangel-Ch, 2004a), often interspersed with ferns such as *Macfadyena ungis*. *Alouatta seniculus* using this community are easily seen because of the very low vegetation, in contrast to other vegetation types.

Rastrojo had a sometimes discontinuous, sometimes continuous canopy and thick undergrowth. Important tree species were *Ficus* spp. (Moraceae), cecropia (*Cecropia* sp., Cecropiaceae), *hobo* (*Spondias mombin*, Anacardiaceae), *copey* (*Clusia* sp., Clusiaceae), *abarco* (*Cariniana pyriformis*, Lecythidaceae), *roble* (*Tabebuia rosea o Taebuia sp.*, Bignoniaceae), *cedro* (*Cedrela* cf. *angustifolia*, *C. odorata,* Meliaceae), *cativo* (*Prioria copaifera*, Caesalpinaceae), *balso* (*Ochromoa pyramidale*, Bombacaceae), *ceiba* (*Ceiba pentandra*, Bombacaceae), *caracolí* (*Anacardium excelsum*, Anacardiaceae), rubber (*Castilla* sp., Moraceae), *churimo* (*Inga* sp. probably *I. edulis*, Mimosaceae). Height of trees in this forest reaches 20–25 m, especially in the cases of *Ceiba pentandra, Anacardium excelsium* and *Jacaranda caucana* (Bignoniaceae). *Rastrojos* are often difficult of access because of the dense and closed vegetation, although some rastrojos were more open and especially exposed along the borders. These forests result from cutting the original forest for agriculture or other purposes and allowing a new forest to grow and mature on the same spot. Rastrojos were often isolated from other forest, requiring terrestrial travel for the *Alouatta* groups.

Gallery forests represented 25% of all observations of *A. palliata*. These primates were found alongside small rivers such as the Chugandi, Negro, Tanela, Tanelita, Cuti, Tibirri and the Titiza among others. Some groups were located in forest bordering very small streams and most of this forest was made up of tall (20-25 m) and continuous vegetation. Common trees of the gallery forest are *balso* (*Ochromoa pyramidale*, Bombacaceae), *guaimaro* (*Brosimum alicastrum* y *B. guianense*, Moraceae), *cedro* (*Cedrela* cf. *angustifolia*, *C. odorata,* Meliaceae), *abarco* (*Cariniana pyriformis*, Lecythidaceae), *caracolí* (*Anacardium excelsum*, Anacardiaceae). DBH´s ranged from 0.63-2.67 m. Gallery forests have been conserved in most of the *veredas* (subdivision of a *municipio* in Colombia), since the inhabitants understand the importance for water quality.

Secondary growth forests showed various states of succession. Disturbances that created clearings modify the structure of the original forest allowing the growth of many pioneer species. Common trees growing in secondary growth forests (similar to *rastrojo*) were *cedro* (*Cedrela* cf. *angustifolia*, *C. odorata,* Meliaceae), *copey* (*Clusia* sp., Clusiaceae), *palma mil pesos* (*Jessenia bataua*, Araceae), *cuipo* (*Cavanillesia platanifolia*, Bombacaceae), *guamo* (*Inga* spp,

Table 4. Altitudinal ranges of sampled sites and the number of sites with either presence or absence of the species.

Landscape type	Elevation (m)	No. Sites	*Alouatta palliata*	*Alouatta seniculus*	Both spp present
Low terraces	0-49	95	42	29	0
Slope	50-99	14	4	0	0
Low hills	100-199	35	26	0	0
Medium hills	200-499	20	9	0	0
Mountains	500-600	0	0	0	0

Table 5. Groups associated with forest types in the study area.

Forest type	*A. palliata*	*A. seniculus*	General total
A. arracachal	0	1	1
A. panganal	1	24	25
Gallery forest	21	0	21
Primary forest	15	0	15
Secondary forest	18	1	19
Cut-over regrowth	26	3	29
General total	81	29	110

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Mimosaceae), *copey* (*Clusia* sp., Clusiaceae) , *yarumo* (*Cecropia* spp., Cecropiaceae), *balso* (*Ochromoa pyramidale*, Bombacaceae) , *tachuelo* (*Zanthoxylum grandifolum*, Rutaceae) and *churimo* (*Inga edulis*, Mimosaceae). These forests were usually surrounded by pasturelands used by cattle.

Primary forests were often disturbed due to logging so that species with low economic value predominated, even though three strata of trees existed. The highest stratum consisted of emergent trees up to 20-25 m, dominated by species such as *higuerón* (*Ficus* sp., Moraceae), *cedro* (*Cedrela* cf. *angustifolia*, *C. odorata* Meliaceae), *caracolí* (*Anacardium excelsum*, Anacardiaceae), *hobo* (*Spondias mombin*, Anacardiaceae), *almendro* (*Dipteryx oleifera*, Fabaceae) and *cordoncillo* (*Piper imperialis*, Piperaceae) among others. This forest type characteristically contained climbing plants and lianas, and very little undergrowth.

Of six forest types, *A. palliata* was found in five and *A. seniculus* in four (Table 5). *A. palliata* was mostly in second growth and gallery forests and never in the arracachal associations (*Montrichardia arborescens*). We observed one group of *A. palliata* in panganal (*Raphia taedigera*). In contrast, *A. seniculus* commonly used the *panganal* association and was seen very rarely in second growth (rastrojo) (Table 5). We never observed either species of *Alouatta* in tree plantations or in other crops, in contrast to *Cebus capucinus*, which we observed several times in both forest plantations and other cultivars.

Discussion

Sympatry

This study confirms the sympatry between *A. seniculus* and *A. palliata* along the west bank of the Atrato river and formally register other sites east of the Atrato river, but we cannot confirm hybridization between the two species. According to local information, sympatry between the two species continues upriver to an undetermined point along the Atrato river. Hybridization is not well-known in *Alouatta*. A study of *Alouatta* sympatry describes hybridization between *A. caraya* and *A. clamitans* in a group of eight individuals observed near the Paraná river in Brazil, in the ecotone between rain forest and the Cerrado, showing intermediate morphological variation (Aguiar *et al.,* 2007). Another study in Tabasco, Mexico, reported hybridization of individuals with a mosaic of morphological characteristics between *A. palliata* and *A. pigra*. These included individuals living in various grades of disturbed vegetation and that had characteristics of both species (Cortes-Ortiz *et al.,* 2007). Also, hybridization is known in captivity between *A. caraya* and *A. guariba* (de Souza *et al.,* 2010).

Habitat preferences

The two species of *Alouatta* in this study are not completely syntopic; their habitat preferences seem to overlap somewhat, affording some contact. According to Agostini *et al.* (2010) in undisturbed habitat the two species could be avoiding competition, employing strategies associated with different diets and different habitat use when in sympatric contact (Lehmann, 2004). Given the differences detected in the use of distinct types of forest in this research and a lack of clear-cut morphological evidence for hybrids, we suspect that the two species maintain effective separation. Further to the east in the highly disturbed and fragmented Colombian Caribbean there may be animals with mixed phenotypes (obs. pers. A. Flórez and F. Garcia-Castillo) and these animals should be studied, especially in Córdoba (Fig. 1). Bicca-Marques *et al.* (2008) indicate that the habitat and utilization of resources are not considered factors that maintain a separation of species of *Alouatta*. Other authors consider that disturbed habitats can play a fundamental role in the sympatry and overlap of species´ ranges (Aguiar *et al.*, 2007, 2008; Agostini, 2010). The situation of the Darien is of a disturbed habitat. Colonization has led to changes in vegetation cover resulting in much pastureland for cattle ranching and disturbed vegetation (Plan de Manejo Katios, 2007). Accordingly it seems logical that these activities might influence contact between the two species.

In the Chocó *A. palliata* was present at all sites sampled from sea level to above 300 m, although its presence in *panganal* was minimal. But *Alouatta seniculus* was absent on the sides of hills from primary and secondary forest, although this species has been found up to 3,200 m in the Colombian Andes and is found in many types of primary forests in the lowlands of Amazonia, as well as gallery forest in Orinoquia and sub-Andean forests in Quindío (Hernández and Cooper, 1975; Gaulin and Gaulin, 1982; Izawa, 1988; Defler, 1981, 2010; Stevenson *et al*., 1991). In the *Darien A. seniculus* is restricted to swampy forest, *panganales* especially along the borders of rivers (Neville 1972; Defler 2010) and it is limited to elevations below 50 m. These uses of particular habitats clearly show there to be a minimum of distribution overlap in the Chocó.

The use of forest strata by *A. palliata* and *A. seniculus* is related principally to the food supply, solar exposure and locomotion (Braza *et al.,* 1981; Lehmann, 2004). These animals prefer forest with adequate connectivity between canopies (Neville, 1972; Izawa, 1976) and tall trees, generally of 20-25 cm diameters or more (Gómez-Posada *et al.,* 2007). The observations of *A. palliata* and *A. seniculus* in this research showed a preference of these primates for upper strata. During the study, *A. palliata* groups were found 77.8% of the time in the canopy. They were only found in underbrush when they were eating from low trees or resting in shade (Palma, 2005). Groups of *A. seniculus* were seen in the low canopy 55% of the times observed where they generally were eating or resting. The middle stratum was used for travel (Izawa, 1976; Braza *et al.,* 1981). They were not observed in tall emergent trees in this study, a contrast to some other studies (Defler, 1981, 2010). The forests that were sampled contained plant species that already have been reported as being highly important for the diet of the

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two species of *Alouatta* (Neville *et al*., 1988). These generally correspond to the Moraceae (usually the most important family in the diet of *Alouatta*) (Milton, 1980; Crockett and Eisenberg, 1987), including especially *Ficus* spp, *Cecropia* spp. as some of the most important genera (Milton, 1980; Gaulin and Gaulin, 1982; Crockett and Eisenberg, 1987; Gómez-Posada *et al*., 2007; Giraldo *et al*., 2007).

Studies of *A. seniculus* suggest that this species is more a generalist than is *A. palliata* and usually does not depend on one type of habitat in particular (Neville, 1972; Stevenson *et al*., 1991; Julliot, 1996; Bicca-Marques, 2003). Other authors report preferences of the species for specific types of vegetation found at riversides, on river terraces, and in transitional forests and forest of Igapó during the dry season (Palacios and Rodríquez, 2001; Iwanaga and Ferrari, 2002) where they consume species such as *Cecropia* sp. and *Ficus* sp. and new leaves (Stevenson *et al.,* 1991). The densest populations known are found in the llanos of Colombia and Venezuela (Crockett and Eisenberg, 1987; Defler (in press-a). In this study *A. seniculus* was associated with vegetation that is frequently inundated and where the species *Raphia taedigera*, *Erythrina fusca* and *Cecropia* sp. were found. Such associations reached heights of only 8-9 m and did not have a continuous stratum along the edge of the Atrato river. This primate was also associated with the plant species *Welfia regia* and *Prioria copaifera* and the animals were often syntopic with *Cebus capucinus*. River and lake-side preferences of *A. seniculus* in eastern Colombia have also been described where no second species of *Alouatta* is present (Defler, in press-a)

A. palliata has demonstrated its capacity for surviving in fragmented habitats (Crockett and Eisenberg, 1987; Clarke *et al*. 2002; Rodríguez-Toledo *et al.,* 2003; Bicca-Marques, 2003). In this study this species seemed quite habituated to human beings, since during the majority of observations they continued their activities without being disturbed by our presence. Nevertheless, hunting of *A. palliata* in some parts of the Darien is reported to be very high, since they are avidly pursued by members of various indigenous ethnic groups such as the Cunas and Emberas (com. pers. various interviewees). Hunting pressure on *A. seniculus* is medium to high along the banks of the Atrato River, according to comments from locals. In other cases, for example around the Ciénega de Ungía and because of the low vegetation, the animals are harassed and chased as a diversion, causing fear towards humans in both cases (probably always a reasonable response).

Conservation issues

The Darien was considered one of the 17 most critical areas in the world for conservation, according to the concept first developed by Myers (1988), underlining the importance of conservation planning and resource management in local development. Human activities compromise the continued presence of howlers in this region, and data on hunting, descriptions of habitat alteration and diseases are relevant for the management and conservation of these species over time. Studies of the ecology of closely related sympatric species represent a challenge, since these relationships are not commonly found in all habitats and their ecological relationships are not always evident. It is particularly important to integrate the demographic history and population structure of these primates to be able to monitor the changes that occur over time (Crockett, 1998; Rodríquez *et al.,* 2003; Asencio *et al*., 2009; Defler, 2010). It is fundamental to define the technical and scientific criteria to be included in any resource planning and to include the active participation of communities in any region for the success of any future studies that facilitate the conservation of these species in the future.

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