



Howlers Are Able to Survive in Eucalyptus Plantations Where Remnant and Regenerating Vegetation Is Available

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Abstract Reversing forest loss through reforestation has become a critical strategy to decrease global climate change, and such programs are more likely to be initiated if they can produce a subsequent monetary gain for the host country. As a result, the planting of monocultures of harvestable trees has become widespread and the practice is accelerating. However, little is known about the effect of such reforestation strategies on biodiversity. Here we quantify the demographic patterns of a population of black howlers (*Alouatta pigra*) living in a 200-ha eucalyptus plantation with connected remnant forests in southeastern Mexico. We compare our results to data from the literature from forest fragments, extensive forest tracts, and different agrosystems. The howler population inhabiting the plantation grew from 69 individuals in 2007 to 77 in 2008 (11.6% growth) and to 84 in 2009 (9.1% growth). During this time the howlers fed extensively on the native vegetation that was growing under the eucalyptus, vines that grew on the plantation trees, and adjacent areas of native secondary growth, but they almost never fed on eucalyptus. Howler

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density in the plantation was greater than in extensive forest tracts or forest fragments, whereas mean group size was similar to that in the forest tracts and greater than in the fragments and agrosystems. There was no apparent difference in the adult female-to-immature ratio among sites. Our results indicate that plantations that have associated native vegetation can play a positive role in the conservation of this species, but suggest that harvesting regimens must be carefully orchestrated to prevent associated food scarcity.

Keywords *Alouatta pigra* · Demography · Eucalyptus · Plantations · Population structure

Introduction

Deforestation and other land-use changes are estimated to have released 150 billion metric tons of carbon into the atmosphere since 1850, *ca.* one fifth of the total carbon in the atmosphere (Houghton 2003). Currently, deforestation accounts for *ca.* 18% of global carbon emissions, which is the third largest source of emissions (IPCC 2007; Keith *et al.* 2009). This has contributed to the fact that Earth's climate has warmed by *ca.* 0.6°C over the past 100 year, and some estimates suggest that the climate could warm up by 5.8°C in this century (IPCC 2001; Walther *et al.* 2002). Recently, there has been a growing appreciation in the academic community and with policymakers of the potential scale of the effect that climate change could have on ecological communities (Hannah *et al.* 2002; McClean *et al.* 2005; Parmesan and Yohe 2003; Pounds *et al.* 1999; van Vliet and Schwartz 2002; Walther *et al.* 2002). This has called for actions to reduce the emissions of carbon and in developing countries has led to the dramatic expansion of plantation (Nair *et al.* 2009). Currently, agroforestry plantations cover *ca.* 187 million ha worldwide (FAO 2009), slightly less than the size of Mexico. Thus, without a doubt, the dramatic expansion of forest plantations is significantly transforming the landscape all over the world (Estades and Temple 1999; Henzi *et al.* 2011; Jackson *et al.* 2005; Zanne and Chapman 2001). However, this has led to concerns about the biodiversity impacts of monoculture plantations (Boyd 2010; Carnus *et al.* 2006; Omeja *et al.* 2011) and the effect of plantations on the neighboring environment, e.g., eucalyptus drying habitats because of elevated evapotranspiration (Jackson and Baker 2010).

There is evidence of the presence of primates in coffee and cacao plantations, orchards, and other agrosystems, where they have been reported to feed on species such as tamarind fruit (*Tamarindus indica*), bananas (*Musa* spp.), and eucalyptus (*Eucalyptus* spp.: Harris and Chapman 2007; Sauter and Cuzzo 2009). For example, 7 primate species occur in agroforestry systems in Indonesia, most notably siamang (*Hylobates syndactylus*) in rubber (*Hevea brasiliensis*) and dammar gum tree plantations (*Shorea javanica*), along with 5 other primate species in durian plantations (*Durio zibethinus*), and the density of these primates in plantations is similar to that in extensive forest tracts (Michon and de Foresta 1995). Similarly, the majority of a strepsirrhine community in eastern Madagascar (*Avahi laniger*, *Cheirogaleus major*, *Hapalemur griseus*, *Indri indri*, *Lemur fulvus*, *Lepilemur mustelinus*, and *Microcebus rufus*) was found in mature eucalyptus plantations

(Ganzhorn 1987). These areas had significant amounts of secondary vegetation offering a source of food; however, the density of these primates in the eucalyptus plantations was low vs. that in tracts of native forest. Finally, the population parameters of some Mesoamerican primates in agrosystems are similar to those of populations in extensive tracts of rain forest (Estrada *et al.* 2006).

Species in *Pinus* and *Eucalyptus* are mostly commonly used in plantations, yet neither is viewed as being overly nutritious (Chapman and Chapman 2002; Rode *et al.* 2003); thus their role in promoting biodiversity is questionable. There are anecdotes of gorillas (*Gorilla gorilla*) eating eucalyptus leaves in spite of their high concentration of secondary metabolites (Boland and Brophy 1993), and recent studies have reported *Eucalyptus* spp. being eaten by black-and-white colobus monkeys (*Colobus guereza*: Harris and Chapman 2007). *Eucalyptus* spp. is also eaten by black-fronted titi monkeys (*Callicebus nigrifrons*: Trevelin *et al.* 2007) and *Alouatta caraya* in South America (Mattjie-Prates and Bicca-Marques 2008).

Some researchers have suggested that forest plantations should include fragments of the native vegetation that would be inhabited by the local plant species. These areas provide sites for foraging, refuge, and buffer zones, in addition to increasing the structural connectivity of the landscape (Greenberg *et al.* 2004; Murphy and Lovett-Doust 2004). For example, in fragments of native vegetation surrounded by a matrix of plantations of *Pinus radiata*, the diversity of birds and arboreal marsupials was greater than in fragments of native vegetation that were not surrounded by pine plantations (Lindenmayer *et al.* 2009).

We evaluated changes in a black howler population living in a eucalyptus plantation in southeastern Mexico over 3 years (2007–2009). We aimed to contribute to an understanding of the biodiversity value of eucalyptus plantations for the conservation of populations of black howlers (*Alouatta pigra*). Given the dramatic expansion of forest plantations, understanding if plantations have a conservation value for black howlers, and if so, what contributes to that value, will provide important information in the construction of informed conservation plans.

Methods

The 200-ha eucalyptus plantation was located in the southern part of the municipality of Balancán in the state of Tabasco, Mexico (17°39'15.319"N and 91°32'13.623"W; altitude: 25 m.a.s.l.). The area is under the stewardship of the rural community and is known as the El Arenal communal lands. The plantation contains *Eucalyptus urophylla*, *E. robusta*, and a hybrid of *E. grandis* and *E. urophylla* (Seppänen 2003; identified and deposited in the XAL Herbarium at the Instituto de Ecología) and is surrounded by pasture (Pozo-Montuy and Serio-Silva 2006; Fig. 1). Mean annual rainfall is 1,850 mm, with little rain falling in the March–May dry season and mean annual temperature is 26.0°C (CNA 2010).

Within the eucalyptus plantation there were 12 fragments of remnant forest (21 ha) running along permanent and ephemeral streams that were dominated by native secondary vegetation that included *Guazuma ulmifolia*, *Cochlospermum vitifolium*, *Cecropia obtusifolia*, *Cordia alliodora*, *Lonchocarpus hondurensis*, and many vines. These multicanopy layered fragments had an understory with areas

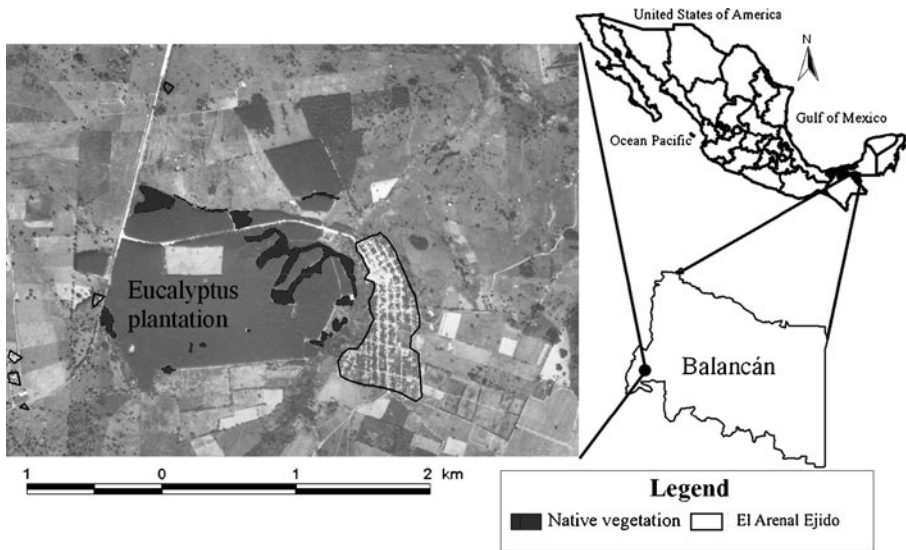


Fig. 1 Location of the El Arenal eucalyptus (*Eucalyptus* spp.) plantation, Balancán, Tabasco, Mexico, where we conducted our 3-yr study of the density and demographics of a population of *Alouatta pigra*. This population was living in a eucalyptus plantation that had access to regenerating natural vegetation in the plantation and areas of regenerating forest adjacent to the eucalyptus. (Source: Orthophotos 1:20000 INEGI 2000 Zone 15, WGRS 80).

covered by woody and herbaceous vines and lianas, shrubs such as *Alibertia edulis*, and young trees, mainly *Orthion subsessile*.

The population of *Alouatta pigra* in this plantation has been studied since 2006 (Díaz-López 2010; Pozo-Montuy and Serio-Silva 2006; Pozo-Montuy et al. 2009; Serio-Silva et al. 2006), and each year between 2007 and 2009 we conducted complete censuses of the 200 ha. Five experienced researchers conducted censuses on foot over several consecutive days each year from 07:00 to 17:00 h. We georeferenced all sightings using a Garmin 12 geopositioning device and plotted them on orthophotos (1:20,000) from 2003 (INEGI 2007) with Arc View 3.3®. We observed each group for ≥ 30 min or until all the members of the research team agreed on the group's composition. We determined the sex and age of each member of the group (adults, juveniles, and infants; the latter 2 age classes are also referred to as immatures) following Pozo-Montuy et al. (2008). We ensured we did not repeat count the same individuals or groups by noting physical characteristics of individuals (scars, coloring, spots on the scrotum and vulva) and the group structure. Additional long-term research being done on the plantation increased the reliability of the data by providing us knowledge of identities of particular individuals in specific groups and home ranges (Bonilla-Sánchez et al. 2010; Díaz-López 2010; Pozo-Montuy and Serio-Silva 2006; Pozo-Montuy et al. 2009; Serio-Silva et al. 2006).

We estimated overall population density (individual/km²) by dividing howler abundance by the total area of the plantation (200 ha). We calculated the finite growth rate (λ) by dividing the population size of a given year by the population size of the previous year, and we used these values to obtain a mean annual finite growth rate. We used λ to calculate the intrinsic growth rate (r) as $r = \ln(\lambda)$ (Arroyo-Rodríguez et al. 2008).

We compared our 2009 data to data from 17 sites in Mexico, Belize, and Guatemala where *Alouatta pigra* were censused (6 in rain forest fragments, 5 in extensive tracts of forest, and 4 in agrosystems, and our study from the eucalyptus plantation). We obtained individual group density of *Alouatta pigra* by dividing group size by mean home range (Pavelka 2003), determined from continuous monitoring of 4 groups in the area (mean home range= $3.8 \pm \text{SD } 0.99$ ha; Bonilla-Sánchez *et al.* unpubl. data; Díaz-López 2010; Estrada *et al.* 2006).

We selected 2 groups (6 and 12 individuals) living in the eucalyptus plantations that were then habituated to observers during 5 month (September 2007–January 2008) before formal data collection. Using focal animal sampling (1 h/individual) we collected data for 15 d/mo from 06:00 to 18:00 h each day during 2 periods of 5 month in 2008 (dry season = February–June; rainy season = August–December; Pozo-Montuy and Serio-Silva 2006). We chose the order in which individuals were observed at random and we tried to record the same number of minutes for each subject per month. We recorded time spent in three main activities (feeding, locomotion, and resting), as well as all occurrences of other less common behaviors (play, grooming, courtship, vocalizations, etc.). Here we present the data on the time spent feeding on different food items based on 886 h (440 and 445 h, respectively) of observation (206 h of feeding).

Results

The population of *Alouatta pigra* in this eucalyptus plantation fed extensively on the native vegetation that was growing under the eucalyptus, vines that grew on the plantation trees, or adjacent areas of native secondary growth (Table I). In fact, we observed them actually feeding on eucalyptus for 0.12% of their feeding time (Table I). The groups are year-round residents of the eucalyptus plantation and move daily between the plantation and remnant forests.

Group size averaged $6.7 \pm \text{SD } 0.2$ individuals across years, but it increased from 6.5 in 2007 to 6.8 in 2008 and 2009. The increase in group size was the result of an increase in the number of adults and immatures in groups and corresponded to an increase in the number of adult females per male (Table II). The number of infants per female and immatures per female both increased over the 3 year (Table II).

There was a gradual increase in the population from 69 individuals (including lone monkeys) in 2007 to 77 in 2008 (11.6%), and 84 in 2009 (2008–2009=9.1%), which meant that the density increased over time as well. The finite growth rate (λ) indicated that mean population size increase was $1.1 \pm \text{SD } 0.02$ per year and the mean annual intrinsic growth rate was $0.10 \pm \text{SD } 0.02$ (Table II).

The number of adult and juvenile males decreased over time, whereas that of infants and female adults increased over time (Table II). We sighted both multimale–multifemale (mean $1.6 \pm \text{SD } 0.1$ adult males/group) and unimale–multifemale (2.6 ± 0.1 adult females/group) social groups, and the multimale groups were larger than unimale groups ($8.2 \pm \text{SD } 0.5$ vs. $5.1 \pm \text{SD } 0.8$ individuals/group). In 2007, the multimale and unimale groups each represented 50.0% of the population, whereas in 2008 and 2009 multimale groups represented 54.5% of all the groups.

Table 1 Tree species ($n=34$) used for food by *Alouatta pigra* during dry and wet seasons in an eucalyptus-secondary forest area in Balancán, Tabasco, Mexico

Scientific name	Family	Items	Dry season		Wet season	
			Minutes	(%)	Minutes	(%)
<i>Chrysophyllum</i> sp.	Sapotaceae	YL, IF	6	0.12	—	—
<i>Casearia nitida</i>	Flacourtiaceae	YL, B	9	0.18	—	—
<i>Cordia alliodora</i>	Boraginaceae	Fl, YL, ML, B	146	2.91	554	7.52
<i>Coccoloba barbadensis</i>	Polygonaceae	YL, B	67	1.33	40	0.54
<i>Faramea occidentalis</i>	Rubiaceae	YL, MF, Fl	250	4.98	13	0.18
<i>Guarea glabra</i>	Meliaceae	YL, MF	2	0.04	8	0.11
<i>Ceiba petandra</i>	Bombacaceae	B	4	0.08	—	—
<i>Inga aff. Belizensis</i>	Fabaceae	B, YL, FL	60	1.19	40	0.54
<i>Miconia argentea</i>	Melastomataceae	IF, MF	521	10.37	—	—
	Fabaceae	YL	—	—	8	0.11
<i>Ficus pertusa</i>	Moraceae	YL, IF, MF, B	335	6.67	8	0.11
<i>Eucalyptus robusta</i>	Myrtaceae	B, MF	—	—	9	0.12
<i>Hymenea courbaril</i>	Leguminosae	YL	—	—	3	0.04
<i>Cecropia obtusifolia</i>	Moreceae	YL, ML, Fl, B, P, St	25	0.50	1066	14.47
<i>Albizia leucocalix</i>	Fabaceae	YL, ML, B, MF, Fl	399	7.94	1,024	13.90
<i>Guazuma ulmifolia</i>	Sterculiaceae	YL, IF, MF	354	7.05	32	0.43
<i>Vitex gaumeri</i>	Verbenaceae	YL, Fl	—	—	31	0.42
<i>Lonchocarpus hondurensis</i>	Fabaceae	YL, ML, B	13	0.26	196	2.66
<i>Piscidia communis</i>	Fabaceae	YL	6	0.12	2	0.03
<i>Astronium graveolens</i>	Anacardiaceae	YL, B	12	0.24	50	0.68
<i>Spondias mombin</i>	Anacardiaceae	YL, ML, B, IF	1	0.02	65	0.88
<i>Lysiloma bahamensis</i>	Fabaceae	YL, B, Fl	76	1.51	364	4.94
<i>Vochysia hondurensis</i>	Vochysiaceae	YL, B, Fl, St	310	6.17	1	0.01
<i>Gmelina arborea</i>	Verbenaceae	YL	1	0.02	—	—
<i>Casimiroa tetrameria</i>	Rutaceae	B	13	0.26	—	—
<i>Bursera simarouba</i>	Simaroubaceae	YL, B, IF	21	0.42	62	0.84
<i>Carica Mexicana</i>	Caricaceae	ML	—	—	111	1.51
<i>Cochlospermum vitifolium</i>	Cochlospermaceae	YL, ML, B, P, Fl	34	0.68	125	1.70
<i>Blepharidium mexicanum</i>	Rubiaceae	YL, ML, Fl	23	0.46	24	0.33
<i>Orthion subsessile</i>	Violaceae	YL, B	9	0.18	7	0.10
<i>Brosimum alicastrum</i>	Moraceae	YL, B, IF, MF, Fl	408	8.12	129	1.75
<i>Zuelania Guidonia</i>	Flacourtiaceae	YL	25	0.50	—	—
<i>Simarouba glauca</i>	Simaroubaceae	MF	7	0.14	—	—
<i>Pouteria unilocularis</i>	-	B	2	0.04	—	—

YL young leaves; ML mature leaves; B buds; IF immature fruits; MF mature fruits; Fl flowers; P petioles; St stems

In 2009, we sighted 84 individuals of *Alouatta pigra* belonging to 12 groups, and there were 3 lone monkeys. Mean group size was $6.8 \pm \text{SD } 1.6$ individuals (mode=7).

Table II Finite growth rate (λ) and other population parameters for black howlers (*Alouatta pigra*) in the El Arenal eucalyptus plantation in Balancán, Tabasco, Mexico

Year	Density ind/ha ^a	λ	r	Abun	AM	AF	JM	JF	IM	IF	LIMM	LM	LF	AF/AM	Imm/AF	Inf/AF
2007	0.35			69	17	26	7	7	1	7	1	2	1	1.5	0.9	0.3
2008	0.39	1.1	0.1	77	19	30	8	8	1	9	2	0	0	1.6	0.9	0.3
2009	0.42	1.1	0.1	84	17	30	4	10	9	11	1	2	0	1.8	1.2	0.7
Mean	0.38	1.1	0.10	76.7	17.7	28.7	6.3	8.3	3.7	9.0	1.3	1.3	0.3	1.6	1.0	0.4
Max	0.42	1.1		84	19	30	8	10	9	11	1	2	1	1.5	0.9	0.7
Min	0.35	1.1		69	17	26	4	7	1	7	2	0	0	1.8	1.2	0.3
SD	0.04	0.02	0.02	7.5	1.2	2.3	2.1	1.5	4.6	2.0	0.6	1.2	0.6	0.1	0.2	0.2

^a Density ind/ha was obtained as result of number of monkeys /200 ha of eucalyptus plantation

λ finite growth rate; r intrinsic growth rate; *Abun* abundance; *AM* adult male; *AF* adult female; *JM* juvenile male; *JF* juvenile female; *IM* infant male; *IF* infant female; *LIMM* lone immature; *LM* lone male; *LF* lone female; *AF/AM* ratio of adult females to adult males; *Imm/AF* ratio of immatures to adult females; *Inf/AF* the number of infants per adult female; *Max* maximum; *Min* minimum; *SD* standard deviation

The population structure was 20% adult males, 36% adult females, 5% juvenile males, 12% juvenile females, and 24% infants. The most frequent social unit was multimale–multifemale ($n=6$), followed by unimale–multifemale ($n=5$), and 1 group had no adult male. This group's male had been killed during timber harvesting, leaving behind 2 adult females and 3 immatures. The average group composition was $1.4 \pm \text{SD } 0.7$ adult males, $2.5 \pm \text{SD } 0.7$ adult females, $0.3 \pm \text{SD } 0.5$ juvenile males, $0.8 \pm \text{SD } 0.6$ juvenile females, $0.8 \pm \text{SD } 0.8$ male infants, and $0.9 \pm \text{SD } 0.9$ female infants per group. In 8 of the 12 groups there were no juvenile males, which accounts for the low mean number of males per group. In these groups, the sex ratio was 1:1.76, the adult female-to-juvenile ratio was 1:0.47, and the ratio of adult females to immatures was 1:1.17.

The howler density in this eucalyptus plantation with its intermingled native regenerating vegetation and adjacent remnant forests was greater than that of protected areas and some fragmented rainforest (Table III). Group density in the eucalyptus plantation was higher than in the extensive forest and fragmented forest sites, but lower than in the other agrosystems, although sometimes not much lower. There were only small differences in the proportion of adult females to immatures between the eucalyptus plantation and the comparison sites. Group size for *Alouatta pigra* in the eucalyptus plantation was very similar to that of howlers that inhabit extensive tracts of forest, but was generally larger than that of those inhabiting forest fragments and other agrosystems. Researchers propose that large howler groups frequent sites with readily available resources (van Belle and Estrada 2006), suggesting that this eucalyptus plantation with its intermingled native regenerating vegetation and adjacent remnant forests was a relatively good habitat for this species. The adult female-to-immature ratio we documented was similar to that reported from a range of other sites, indicating that the habitat was relatively good.

Discussion

If we consider the population changes as an adaptive response to the environment and that the demographic changes in the eucalyptus plantation does not represent a regional phenomenon, such as 3 year of favorable weather, the population growth, continuity of reproduction, relatively large group size, and the adult female-to-immature ratios we documented all suggest that black howlers were successfully exploiting the resources available in the eucalyptus plantation complex and thus that they are a viable population in this habitat. This raises the question of how they are able to thrive when it is well known that eucalyptus plant parts have high levels of secondary metabolites (Foley and Moore 2005). The answer appears to rest in the fact that the howlers are not directly consuming the eucalyptus, but instead are eating resources that grow on the trunks of the eucalyptus trees: plants such as the vine *Syngonium podophyllum* and the numerous trees *Cecropia obtusifolia* in the understory (Asensio et al. 2009; Dunning et al. 1992).

Our observations suggest that howlers do no notable damage in plantations and that plantations could actually benefit from their presence. Folivorous primates may accelerate energy and nutrient flow because their dung contains concentrations of nitrogen and phosphorus that are higher than that of the decomposing organic matter (Nagy and Milton 1979). Also, when the howlers eat the vines that grow on the

Table III Reports of *Alouatta pigra* in fragmented rain forest, extensive tracts of rain forest, and agrosystems

Sites	Mean group size (no. of ind.)	± SD	AF:IMM	Density (ind/ha)	Source
Rain forest fragments					
CBS	5.6	0.6	1.08	1.23	Ostro <i>et al.</i> 2001
Monkey River	6.6	2.8	1.48	1.02	Pavelka 2003
Lachúa	5.2	2.0	0.98	1.70	Rosales-Meda <i>et al.</i> 2007
Palenque	5.9	3.1	1.48	1.19	Estrada <i>et al.</i> 2002
Catazajá	5.0	2.1	0.80	0.95	Bonilla-Sánchez <i>et al.</i> 2010
Balancán	6.0	2.0	1.00	0.18	Pozo-Montuy <i>et al.</i> 2008, 2011
Extensive tracts of rain forest					
PNP	6.7	2.8	1.61	0.23	Estrada <i>et al.</i> 2002
Tikal	8.8	2.2	1.38	0.17	Estrada <i>et al.</i> 2004
LLNP	5.6	1.8	1.21	0.15	Van Belle and Estrada 2006
Calakmul	7.5	1.9	1.38	0.15	Estrada <i>et al.</i> 2004
Yaxchilán	6.6	2.1	1.04	0.12	Estrada <i>et al.</i> 2004
Tormento	6.7	2.3	1.10	0.12	Barrueta <i>et al.</i> 2003
Agrosystems					
Lachúa-cardamom	5.4	1.8	1.08	0.59	Estrada <i>et al.</i> 2006
Balancán-orchards	4.9	2.3	1.11	6.75	Pozo-Montuy <i>Unpubl data</i>
Balancán-isolated trees ^a	5.3	2.6	1.04	3.30	Pozo-Montuy <i>Unpub. data</i>
Balancán-living fences	4.5	2.6	0.50	4.30	Pozo-Montuy <i>Unpubl data</i>
Eucalyptus plantation	7.0	1.6	1.17	1.17 ^b	This study

Group size, the adult female-to-immature ratio (AF:IMM), and monkey density are reported according to the literature

^a Isolated trees in pastures to provide shade for cattle

^b No. of monkeys per troop/home range average (3.8±0.99 ha)

ind individuals; *SD* standard deviation; *CBS* Community Baboon Sanctuary; *PNP* Palenque National Park; *LLNP* Laguna Lachúa National Park

trunks of the eucalyptus they are effectively controlling the growth of species that compete with the plantation trees for nutrients (Laurance *et al.* 2000).

In spite of this potential for mutual benefit between the howlers and the eucalyptus, the situation is likely not sustainable because plantations are harvested, which typically removes all large eucalyptus trees and destroys or damages native trees (Omeja *et al.* 2009, 2011). At El Arenal it was clear that the company in charge was managing the plantation inappropriately: there was a lack of security and lax adherence to regulations. This company was not adhering to restrictions that limited use of a 25-m buffer zone between the native vegetation and the eucalyptus trees (Araujo 1995) and allowed heavy machinery to go through these remnants, sending eucalyptus litter into the streams and into secondary vegetation. The company also did not directionally fell the eucalyptus trees away from native trees or even from trees occupied by howlers.

Our data suggest that howlers can survive and apparently thrive in eucalyptus plantations where remnant and regenerating vegetation is available, suggesting that plantations could be incorporated into conservation and management strategies for primates. In addition, plantations are often established in grasslands that are often formerly forest; they represent a fast growing timber resource that prevents soil erosion, contributes to atmospheric carbon fixation, has a monetary value that can pay for the reforestation, and in the long-term could increase connectivity among isolated forest fragments of rain forest (Cristinacce *et al.* 2009; Duncan and Chapman 2003; Ganzhorn 1987; Zanne and Chapman 2001). However, plantations are typically private initiatives (Pérez-Vera *et al.* 2005), frequently planted on leased lands, and the managers' objective is to maximize profit by harvesting as many eucalyptus trees as possible. In such cases there is little or no thought to rotation, sustainable development, or avoiding negative effects on the animals that inhabit the plantation. Lindenmayer *et al.* (2009) evaluated the effects of the harvest of a plantation of *Pinus radiata* surrounding fragments of native vegetation in Australia and reported considerable decreases in marsupial and avian diversity where a total harvest was conducted compared with sites where the harvest was gradual. This kind of total harvest creates a strong edge effect and leaves the plants and animals with no protection from wind or severe weather events (Foggo *et al.* 2001; Laurance *et al.* 1998). These studies and ours indicate that if plantations are to have a conservation function, companies and landowners should be required to protect native vegetation and rotate the harvest such that fragments of native vegetation are not suddenly left completely devoid of the matrix that surrounds them.

When considering any conservation action, it is critical to take a very broad perspective and not simply focus on the effects of planned intervention on a single taxonomic group of interest, in this case primates. The effects of plantations on the ecosystem responses are often site specific (Close *et al.* 2011); however, in general trees use more water than co-occurring herbaceous and grassland species (Engel *et al.* 2005), and eucalyptus species are particularly water demanding (Jackson and Baker 2010). For example, plantations, in general, reduce total annual stream flow by 38% vs. grasslands (Jackson and Baker 2010). Further, frequent harvesting of plantations can reduce nutrient availability (Jackson *et al.* 2005). Thus, although our data indicate that eucalyptus plantations where remnant and regenerating vegetation is available are suitable for howlers over the short term, they may not be suitable for other species or not suitable for howlers in the long term. For example, in this region with a prolonged dry season and only 1,850 mm of rainfall annually, eucalyptus may cause excessive drying, making the area unsuitable for some native vegetation required by howlers, or over the long term the eucalyptus may deplete soil nutrients, making the habitat unsuitable for some native plant species. These sorts of possible linkages need to be investigated in the future.

With the appropriate management strategy that guards against excessive habitat desiccation or nutrient depletion, plantations could protect neighboring native vegetation (Duncan and Chapman 2003) and could replace other types of matrix that are less suitable to native fauna, such as cattle pastures. Eucalyptus trees are not the only species suitable to use in management strategies advocating the use of plantations; there are many fast-growing native species that could be used profitably to extend the habitat of the howlers. Howlers, in addition to using these plantations

as a surrogate structural habitat, could feed in these tree species, but benefits of this foraging activity would need to be evaluated against costs of reduced plantation profits.

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References

- Araujo, M. B. (1995). The effect of *Eucalyptus globulus* Labill. plantations on biodiversity: a case study in Serre de Portel (South Portugal). University College London.
- Arroyo-Rodríguez, V., Asensio, N., & Cristóbal-Azkarate, J. (2008). Demography, life history and migrations in a Mexican mantled howler group in a rainforest fragment. *American Journal of Primatology*, *70*, 114–118.
- Asensio, N., Arroyo-Rodríguez, V., Dunn, J., & Cristóbal-Azkarate, J. (2009). Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica*, *41*, 768–773.
- Barrueta, R. T., Estrada, A., Pozo, C., & Calmé, S. (2003). Reconocimiento demográfico de *Alouatta pigra* y *Ateles geoffroyi* en la Reserva El Tormento, Campeche, México. *Neotropical Primates*, *11*, 165–169.
- Boland, D. J., & Brophy, J. J. (1993). Essential oils of the eucalypts and related genera. In R. Teranishi, R. G. Buttery, & H. Sugisawa (Eds.), *Bioactive volatile compounds from plants* (pp. 72–87). Washington, DC: American Chemical Society.
- Bonilla-Sánchez, Y. M., Serio-Silva, J. C., Pozo-Montuy, G., & Bynum, N. (2010). Population status and identification of potential habitats for the conservation of the black howler monkey in northern of Chiapas, Mexico. *Oryx*, *44*, 293–299.
- Boyd, E. (2010). Societal choice for climate change futures: Trees, biotechnology and clean development. *Bioscience*, *60*, 742–750.
- Carnus, J. P., Parrotta, J., Brockerhoff, E., Arbez, M., Hactel, H., Kremer, A., et al. (2006). Planted forests and biodiversity. *Journal of Forestry*, *104*, 65–77.
- Chapman, C. A., & Chapman, L. J. (2002). Foraging challenges of red colobus monkeys: Influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology. Part A, Physiology*, *133*, 861–875.
- Close, C. C., Davidson, N. J., & Swanborough, P. W. (2011). Fire history and understorey vegetation: Water and nutrient relations of *Eucalyptus bomphocephala* and *E. delegatensis* overstorey trees. *Forest Ecology and Management*, *262*, 108–214.
- CNA. (2010). Comisión Nacional del Agua. www.cna.gob.mx.
- Cristinacce, A., Switzer, R. A., Cole, R. E., Jones, C. G., & Bell, D. J. (2009). Increasing use of exotic forestry tree species as refuges from nest predation by the critically endangered Mauritius fody *Foudia rubra*. *Oryx*, 97–103.
- Díaz-López, H. M. (2010). *Uso del espacio horizontal y vertical por Alouatta pigra en el dosel de plantaciones agroforestales de eucalipto (Eucalyptus grandis) en Balancán*. Tabasco: Universidad Juárez Autónoma de Tabasco.
- Duncan, R. S., & Chapman, C. A. (2003). Consequences of plantation harvest during tropical forest restoration in Uganda. *Forest Ecology and Management*, *173*, 235–250.
- Dunning, J. B., Danielson, B. J., & Pulliam, R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 196–175.
- Engel, V., Jobbagy, E. G., Stieglitz, M., Williams, M., & Jackson, R. B. (2005). Hydrological consequences of Eucalyptus afforestation in the Argentine Pampas. *Water Resources Research*, *41*, 1–14.
- Estades, C. F., & Temple, S. A. (1999). Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecological Applications*, *9*, 573–585.

- Estrada, A., Castellanos, L. Y. G., Franco, B., Muñoz, D., Ibarra, A., et al. (2002). Survey of the black howler monkey, *Alouatta pigra*, population at the Mayan site of Palenque, Chiapas, Mexico. *Primates*, *44*, 51–58.
- Estrada, A., Garber, P. A., Pavelka, M. S. M., & Luecke, L. (2006). Overview of the Mesoamerican primate fauna, primate studies, and conservation concerns. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation* (pp. 1–22). New York: Springer.
- Estrada, A., Luecke, L., Van Belle, S., Barrueta, E., & Rosales-Meda, M. (2004). Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilan, Mexico and Tikal, Guatemala. *Primates*, *45*, 33–39.
- Estrada, A., Mendoza, A., Castellano, L., Pacheco, R., Van Belle, S., García, Y., et al. (2002). Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, México. *American Journal of Primatology*, *58*, 45–55.
- FAO. (2009). <http://www.fao.org>.
- Foggo, A., Ozanne, C. M. P., Speight, M. R., & Hambler, C. (2001). Edge effects and tropical forest canopy invertebrates. *Plant Ecology*, *153*, 347–359.
- Foley, W. J., & Moore, B. D. (2005). Plant secondary metabolites and vertebrate herbivores from physiological regulation to ecosystem function. *Current Opinion in Plant Biology*, *8*, 430–435.
- Ganzhorn, J. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology*, *12*, 205–215.
- Greenberg, R., Bichier, P., & Cruz, A. (2004). Bird conservation value of cacao plantations with diverse planted shade in Tabasco, Mexico. *Animal Conservation*, *22*, 105–112.
- Hannah, L., Midgley, G. F., Lovejoy, T., Bond, W. J., Bush, M., Lovett, J. C., et al. (2002). Conservation of biodiversity in a changing climate. *Conservation Biology*, *16*, 264–268.
- Harris, T. R., & Chapman, C. A. (2007). Variation in the diet and ranging behavior of black-and-white colobus monkeys: Implications for theory and conservation. *Primates*, *28*, 208–221.
- Henzi, S. P., Brown, L. R., Barrett, L., & Marais, A. J. (2011). Troop size, habitat use, and diet of chacma baboons (*Papio hamadryas ursinus*) in commercial pine plantations: Implications for management. *International Journal of Primatology*, *32*, 1020–1032.
- Houghton, R. A. (2003). Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus*, *55*, 378–390.
- INEGI (2007). Instituto Nacional de Estadística, Geografía e Informática. Visualizador de ortofotos. <http://mapserver.inegi.org.mx/map/visorDx/visor.html?c=1379&s=geo>
- IPCC. (2007). *Climate change 2007: Synthesis report*. Geneva: Intergovernmental Panel on Climate Change.
- IPPC. (2001). *Climate change 2001: The scientific basis*. Cambridge, UK: Cambridge University Press.
- Jackson, R. B., & Baker, J. S. (2010). Opportunities and constraints for forest climate mitigation. *BioScience*, *60*, 698–707.
- Jackson, R. B., Jobbagy, E. G., Avissar, R., Roy, S. B., Barrett, D. J., Cook, C. W., Farley, K. A., le Maitre, D. C., McCarl, B. A., & Murray, B. C. (2005). Trading water for carbon with biological sequestration. *Science*, *310*, 1944–1947.
- Keith, H., Mackey, B. G., & Lindenmayer, D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences of the USA*, *106*, 11635–11640.
- Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., & Laurance, S. G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, *79*, 2032–2040.
- Laurance, W. F., Vasconcelos, H. L., & Lovejoy, T. E. (2000). Forest loss and fragmentation in the Amazon: Implications for wildlife conservation. *Oryx*, *34*, 39–45.
- Lindenmayer, D. B., Wood, J. T., Cunningham, R. B., Crane, M., MacGregor, C., Damian, M., et al. (2009). Experimental evidence of the effects of a changed matrix on conserving biodiversity within patches of native forest in an industrial plantation landscape. *Landscape Ecology*, *24*, 1091–1103.
- Mattjie-Prates, H., & Bicca-Marques, J. C. (2008). Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an Orchard Forest. *International Journal of Primatology*, *29*, 703–715.
- McClellan, C. J., Lovett, J. C., Kuper, W., Hannah, L., Sommer, J. H., Barthlott, W., et al. (2005). African plant diversity and climate change. *Annals of the Missouri Botanical Gardens*, *92*, 139–152.
- Michon, G., & de Foresta, H. (1995). The Indonesian agro-forest model. In P. Halladay & D. A. Gimour (Eds.), *Conserving biodiversity outside protected areas: The role of traditional agroecosystems*. Gland, Switzerland: IUCN.
- Murphy, H. T., & Lovett-Doust, J. (2004). Context and connectivity in plant populations and landscape mosaics: Does the matrix matter? *Oikos*, *105*, 3–14.

- Nagy, K. A., & Milton, K. (1979). Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology*, *60*, 475–480.
- Nair, P. K. R., Nair, V. D., Kumar, B. M., & Haile, S. G. (2009). Soil carbon sequestration in tropical agroforestry systems: A feasibility appraisal. *Environmental Science and Policy*, *12*, 1099–1111.
- Omeja, P. A., Chapman, C. A., & Obua, J. (2009). Enrichment planting does not promote native tropical tree restoration in a former pine plantation. *African Journal of Ecology*, *47*, 650–657.
- Omeja, P. A., Chapman, C. A., Obua, J., Lwanga, J. S., Jacob, A. L., Wanyama, F., et al. (2011). Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation. *Forest Ecology and Management*, *261*, 703–709.
- Ostro, L., Silver, S. C., Koontz, F. W., Horwich, R. H., & Brockett, R. (2001). Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. *International Journal of Primatology*, *22*, 733–748.
- Parnesan, C., & Yohe, G. A. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42.
- Pavelka, M. S. M. (2003). Group, range, and population size of *Alouatta pigra* at Monkey River, Belize. *Neotropical Primates*, *11*, 187–191.
- Pérez-Vera, O. A., Yañez-Morales, M. J., Alvarado-Rosales, D., Cibrian-Tovar, D., & García-Díaz, S. E. (2005). Hongos asociados a Eucalipto, *Eucalyptus grandis* Hill: Maid Fungi. *Agrociencia*, *39*, 311–318.
- Pounds, J. A., Fogden, M. P. L., & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, *398*, 611–615.
- Pozo-Montuy, G., Bonilla-Sánchez, Y. M., Díaz-López, H. M., & Serio-Silva, J. C. (2009). Estudio poblacional de monos aulladores negros *Alouatta pigra* habitando dentro de plantaciones de Eucalipto en Balancán, Tabasco. Paper presented at the IV Congreso Mexicano de Primatología, Villahermosa, Tabasco, México.
- Pozo-Montuy, G., & Serio-Silva, J. C. (2006). Comportamiento alimentario de monos aulladores negros (*Alouatta pigra* Lawrence Cebidae) en hábitat fragmentado en Balancán Tabasco México. *Acta Zoologica Mexicana ns*, *22*, 53–66.
- Pozo-Montuy, G., Serio-Silva, J. C., & Bonilla-Sánchez, Y. M. (2011). The influence of the matrix on the survival of arboreal primates in fragmented landscapes. *Primates*, *52*, 139–147.
- Pozo-Montuy, G., Serio-Silva, J. C., Bonilla-Sánchez, Y. M., Bynum, N., & Landgrave, R. (2008). Current status of the habitat and population of the black howler monkey (*Alouatta pigra*) in Balancán, Tabasco, Mexico. *American Journal of Primatology*, *70*, 1–8.
- Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. (2003). Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology*, *24*, 541–573.
- Rosales-Meda, M., Estrada, A., & López, J. E. (2007). Demographic survey of black howler monkey (*Alouatta pigra*) in the Lachuá Eco-region in Alta Verapaz, Guatemala. *American Journal of Primatology*, *70*, 231–237.
- Sauther, M. L., & Cuzzo, F. P. (2009). The impact of fallback foods on wild ring-tailed lemurs biology: A comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology*, *140*, 671–686.
- Seppänen, P. (2003). Costo de la captura de carbono en plantaciones de eucalipto en el trópico. *Foresta Veracruzana*, *5*, 1–6.
- Serio-Silva, J. C., Pozo-Montuy, G., & Bonilla-Sánchez, Y. M. (2006). Black howler monkeys (*Alouatta pigra*) inhabiting eucalyptus (*Eucalyptus grandis*) plantations in Tabasco, Mexico: Habitat use and questions to answer. *American Journal of Primatology*, *68*, 35.
- Trevelin, L. C., Port-Carvalho, M., Silveira, M., & Morell, E. (2007). Abundance, habitat use and diet of *Callicebus nigrifrons* Spix (Primates, Pitheciidae) in Cantareira State Park, São Paulo, Brazil. *Revista Brasileira de Zoologia*, *24*, 1071–1077.
- van Belle, S., & Estrada, A. (2006). Demographic features of *Alouatta pigra* populations in extensive and fragmented forest. In A. Estrada, P. Garber, M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 121–142). New York: Kluwer Academic/Plenum Press.
- van Vliet, A., & Schwartz, M. D. (2002). Phenology and climate: The timing of life cycle events as indicators of climate variability and change. *International Journal of Climatology*, *22*, 1713–1714.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., et al. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.
- Zanne, A. E., & Chapman, C. A. (2001). Expediting reforestation in tropical grasslands: Distance and isolation from seed sources in plantations. *Ecological Applications*, *11*, 1610–1621.