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Focusing Conservation Efforts for the Critically Endangered Brown-headed Spider Monkey (*Ateles fusciceps*) Using Remote Sensing, Modeling, and Playback Survey Methods

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Abstract Brown-headed spider monkeys (*Ateles fusciceps*), endemic to the Choco-Darien forests and lower Andean forests of NW Ecuador, are considered critically endangered. Unfortunately, scientific data regarding the actual status of populations is lacking. We combined satellite image analysis, species-specific habitat assessment, and a field survey technique using playback to focus conservation efforts for this species. First, we identified remaining forest via a LANDSAT mosaic and then applied species-specific criteria to delineate remaining forest with potential to hold populations. By combining this with the historical distribution from ecological niche modeling and predicted hunting intensity we generated a species-specific landscape map. Within our study area, forest capable of sustaining *Ateles fusciceps* covers 5872 km^2, of which 2172 km^2 (40%) is protected. Unprotected forest considered suitable for *Ateles fusciceps* extends to 3700 km^2 but within this only 989 km^2 (23%) is under low hunting pressure and likely to maintain healthy populations of *Ateles fusciceps*. To overcome problems of sampling at low primate density and in difficult mountain terrain we developed a field survey technique to determine

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presence and estimate abundance using acoustic sampling. For sites under low hunting pressure density of primates varied with altitude. Densities decreased from 7.49 individuals/km^2 at 332 masl to 0.9 individuals/km^2 at 1570 masl. Based on combining data sets in a gap analysis, we recommend conservation action focus on unprotected lowland forest to the south and west of the Cotacachi-Cayapas Ecological Reserve where hunting pressure is low and population densities of *Ateles fusciceps* are greatest.

Keywords *Ateles fusciceps* · Brown-headed spider monkey · Ecological niche modeling · Habitat mapping · LANDSAT · MaxEnt

Introduction

Brown-headed spider monkeys (*Ateles fusciceps*), endemic to Ecuador and southern Colombia, are critically endangered (A2cd) owing to small population size, restricted distribution, and the pressures facing remaining populations (Cuarón et al. 2008; Tirira 2001). They inhabit the evergreen humid tropical forests of the Pacific coastal zone that make up the Chocó ecoregion, with populations in the Andean foothills that extend into the western Andean ecoregion. It is estimated that in Ecuador there are <250 individual *Ateles fusciceps* in the wild (Tirira 2004), with populations restricted to the Awa Indigenous Reserve at the border with Colombia, and the Cotacachi-Cayapas Ecological Reserve and buffering protected forests (Mittermeier *et al*. 1997; Tirira 2007). Population decline is due to hunting and high rates of deforestation in a region where destruction of the humid tropical forest has resulted in a loss of >80% of its original area (Tirira 2004). Unfortunately, the ecology and life history of *Ateles fusciceps* facilitates threats to its survival. First, these primates are known to inhabit only large continuous areas of primary forest (Defler 2004), or forest of ≥60 yr of age (Sorensen and Fedigan 2000). Second, spider monkeys have a relatively low reproductive rate for neotropical species, owing to an extended interbirth interval of 2–3 yr. This hinders their ability to recover from loss of numbers (Ross and Jones 1999; Tirira 2007).

In 2000, Ecuadorian legislation banned the hunting and commercial use of *Ateles fusciceps* (Tirira 2007). After this major breakthrough, the Convention on International Trade in Endangered Species (CITES) up-listed *Ateles fusciceps* to Appendix II of the Convention on International Trade in Endangered Species (CITES). This ensures that any international trade of the species requires legal permits (CITES 2007). However, the actual impact of these national and international legislative measures on the conservation status of primate populations in the isolated forests of NW Ecuador is unknown.

Of the 2 remaining forest blocks with recorded populations of *Ateles fusciceps*, the best hope for the long-term survival of populations is the Cotacachi-Cayapas Ecological Reserve (see Fig. 2). Pressures from logging, road construction, and hunting are very high in the other remaining forest block, the Awa Reserve, and likely to increase in the future (Tirira 2001, 2004). The major challenge to developing a conservation action plan for *Ateles fusciceps* is the dearth of knowledge regarding this primate. Targeted conservation effort to save remaining populations is currently hampered by a lack of information regarding the distribution and status of remaining populations and the spatial distribution of the threats they face. To implement conservation programs data are urgently required to:

- Determine the distribution and abundance of remaining populations of *Ateles fusciceps*
- Identify the spatial pattern of pressures facing these remaining populations

We aim here to focus conservation efforts by combining satellite, modeling, and field data. The objectives are to map remaining forest using LANDSAT satellite imagery, determine potential primate distribution in these forests via ecological niche modeling, identify protected forests, and predict hunting levels. We also provide the first field abundance data, using an acoustic sampling method, to determine primate density throughout the pronounced altitudinal gradient of these Andean forests.

There are inherent practical difficulties in determining the abundance of primates at low densities in isolated and rugged tropical forest terrain. The most frequently used technique for estimating primate population densities in the neotropics is the line transect method (Ross and Reeve 2003), which involves visual counts and is commonly analyzed via DISTANCE methods (Buckland *et al*. 1993; Thomas *et al*. 2005). This method becomes difficult to apply to rare, widely dispersed, and elusive species such as *Ateles fusciceps* in mountainous terrain. In particular, the time taken and distances that must be covered before confident estimates of population can be attained are prohibitive owing to the challenging terrain. Despite this limitation, line transect surveys of *Ateles fusciceps* at the Los Cedros Biological Reserve (00°18′19″ N, 78°46′28″W) identified a population density of 1.16 individuals/km^2. However, to obtain this estimate, field workers needed to traverse a total of 820.5 km over 981 h (Gavilanez-Endara 2006). Perhaps more importantly, working in mountainous terrain often invalidates a critical assumption of DISTANCE sampling: that of randomized transects. The density estimates can be seriously biased because of steep slopes that force transects to follow ridges. As standard survey methods prove nearly impossible to apply, both statistically and physically, there is the urgent need to develop site-specific or species-specific survey tools.

Auditory methods provide a solution to some of these difficulties. A number of studies employ auditory methods in population surveys of primates with extensive and regular vocal repertoires (Estrada *et al*. 2004). Calls can be used to detect individuals from greater distances than is possible through sightings, and the use of auditory cues increases the number of encounters. In the neotropics, howlers produce loud calls most mornings, allowing researchers to identify the minimum number of groups using sound-based methods (Estrada *et al*. 2004). Where regular calls do not form part of the behavior of targeted species, playback of recordings of particular vocalizations may elicit a vocal response, e.g., in field surveys of golden-headed tamarins in Brazil (Pinto and Rylands 1997). From anecdotal evidence it is known that *Ateles fusciceps* responds to hunters who mimic their alarm call. As a result, we wanted to determine the viability of using their vocal response to playback as a rapid survey tool to determine presence, and provide estimates of their abundance.

A number of studies show that primate population density tends to decrease with increasing altitude and attributed this to a reduction in food density and quality at higher altitudes (Caldecott 1980; Durham 1975; Marshall *et al*. 2005). We developed and applied a playback method to generate the first data set of *Ateles fusciceps* density against altitude, as remaining forests in the region range in altitude from sea level to the altitudinal limit of *A. fusciceps*.

One of the major pressures facing populations of *Ateles fusciceps* is hunting. Spider monkeys are the largest bodied primate genus of the neotropics (Defler 2004), estimated to comprise between 11.5% and 2.4% of the mammalian biomass in neotropical forests (Peres and Dolman 2000; Redford 1992). Their size and flesh, considered flavorful (Tirira 2001), makes them prime targets for hunting. They also feature prominently in the illegal pet trade (Estrada and Mandujano 2003). It is difficult to ascertain actual hunting levels, particularly as hunting of *Ateles fusciceps* is now illegal in Ecuador. We incorporated a simplified model of hunting activity based on the location of human settlements to map risk to *Ateles fusciceps*.

A gap analysis using a combination of the first altitudinal field data set of abundance for this primate species, satellite analysis of remaining forest, and modeling and mapping data provide the opportunity to identify regions requiring urgent conservation action to protect remaining populations of *Ateles fusciceps*.

Materials and Methods

Through supervised classification of LANDSAT satellite imagery we identified remaining forest in the study region. As the major challenge is abundant and persistent cloud cover, we needed to use select LANDSAT imagery (Table I). Using ERDAS Imagine 8.3 we first deleted cloud from all LANDSAT images and then conducted supervised classification on cloud-free imagery to generate thematic map categories of cloud shadow, water, urban/cleared land, pasture/crop, agriculture, and forest. Classification was guided by ground truthing (collecting GPS coordinates of the land categories) and reference to maps and aerial imagery available from the Instituto Geografico Militar, Quito, Ecuador. The resulting mosaic, generated in ESRI ArcGIS 9.2, best represents remaining forest from the thematic maps.

Table I LANDSAT images used in forest status classification

Row	Path	Satellite sensor	Date of image
10	59	ETM+	May 25, 2006[a]
10	60	ETM+	May 25, 2006[b]
10	60	ETM+	August 13, 2006[c]
10	60	ETM+	November 3, 2001[d]
10	60	TM	March 23, 1988[d]

[a] Gap filled with 18 02 2006 SLC–Off and 24 03 2001 SLC–On

[b] Gap filled with 18 02 2000 SLC–ON and 03 11 2001 SLC–On

[c] Gap filled with 09 07 2005 SLC–Off and 03 11 2001 SLC–ON

[d] Source for this data set was the Global Land Cover Facility (www.landcover.org)

To maintain a population of *Ateles fusciceps*, forest needs to be at least as large as the home range for this primate. With no home range information available for *Ateles fusciceps*, we conservatively applied a value close to the largest recorded home range reported for *Ateles*, 469 ha for *Ateles belzebuth* in the Ecuadorian Amazon (Pozo 2001). We generated a forest suitability map for *Ateles fusciceps* based on a circular moving window to represent home range. In this new map, each pixel of 30 m^2 resolution represents the percentage of forest within a radius of 1200 m, equivalent to an area of 452 ha. We defined forest suitable for *Ateles fusciceps* at each pixel if forest represented 80% of the area within the 1200 m radius, and where cloud cover and shadow contributed <25%. These criteria are arbitrary but allow for a small amount of cloud cover or misclassification. We assume that if 80% of the classifiable window comprises forest, the remainder has a high probability of being forest cover as well and will be suitable for the primate. The resultant data layer maps remaining forest capable of containing *Ateles fusciceps*, assuming no other factors impact numbers.

MaxEnt is a general-purpose method for generating predictions or inferences from incomplete information. It is an empirical modeling approach, based on indirect and direct variables (Guisan and Zimmermann 2000). The model generates probabilities of species occurrence across the entire study region based on a suite of environmental variables, e.g., precipitation, temperature, altitude, and species locality data. MaxEnt requires presence-only data, using a random selection of background pixels from the study area as pseudo-absences (Phillips *et al*. 2006). We selected species localities from records of *Ateles fusciceps* collected between 1995 and 2008 (Tirira 1995–2008). We excluded localities from the data set if they fell above an altitude of 1800 m, considered the limit for this particular spider monkey (Tirira 2007). Further, we deleted points if they clustered within a 5-km radius of each other to minimize impacts of spatial autocorrelation (Segurado *et al*. 2006). In these cases we used only 1 point to represent presence in the area. We applied a total of 17 selected localities, along with 20 environmental variables comprising temperature, precipitation, and altitude to the MaxEnt model (Table II). We tested the ability of the model to make better than random predictions using a jackknife validation method (Pearson *et al*. 2007). The jackknife method removes 1 locality point from the data set and the model and rebuilds the model using the remaining $n-1$ localities. Thus for a species with n localities, the jackknife method builds n individual models for testing. For *Ateles fusciceps* the jacknife method builds 17 test models. We evaluated the accuracy and significance of the model by its ability to predict the 1 excluded test locality as present (Pearson *et al*. 2007). Using all 17 localities to gain a best-fit model across the entire study region, we predicted the historical distribution. We then projected the resulting distribution in ArcGIS 9.2 for spatial analysis and visual representation.

To model hunting activity we first identified human settlements from georeferenced 1:250000 maps (Ibarra NA-17-16, Esmereldas NA-17-15, San Lorenzo NA-17-12, Instituto Geografico Militar, Quito, Ecuador). We applied buffers around these settlements to identify the extent of hunting. We used a buffer radius of 9 km for lowland settlements (<600 masl) (Peres 1990; Peres and Dolman 2000) and a 3-km buffer (Diego Tirira *pers. com.*) for highland settlements (>600 masl) where mountainous terrain is less amenable to hunting forays. We chose the buffers based

Table II Environmental layers used in distribution modeling: Bioclimatic variables

Environmental data
BIO1: Annual mean temperature
BIO2: Mean diurnal temperature range (mean of monthly: max temp–min temp)
BIO3: Isothermality (BIO2/BIO7)
BIO4: Temperature seasonality
BIO5: Maximum temperature of warmest month
BIO6: Minimum temperature of coldest month
BIO7: Temperature annual range (BIO5–BIO6)
BIO8: Mean temperature of wettest quarter
BIO9: Mean temperature of driest quarter
BIO10: Mean temperature of warmest quarter
BIO11: Mean temperature of coldest quarter
BIO12: Annual precipitation
BIO13: Precipitation of wettest month
BIO14: Precipitation of driest month
BIO15: Precipitation seasonality (Coefficient of Variation)
BIO16: Precipitation of wettest quarter
BIO17: Precipitation of driest quarter
BIO18: Precipitation of warmest quarter
BIO19: Precipitation of coldest quarter
Altitude

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on published information and expert knowledge, but we also investigated the impact on the model of combinations of larger buffers of 13.5 km and 18 km for low-altitude settlements and 4.5-km and 6-km for high-altitude settlements.

We developed a rapid survey method to determine presence and estimate abundance of *Ateles fusciceps* using acoustic sampling methods. We recorded alarm calls of *Ateles fusciceps* at the Los Cedros Reserve (0°18′N, 78°47′W) using a Marantz PMD 222 portable cassette recorder and an 800 series Audio-technica directional microphone. We captured 4 alarm calls and recorded them to 90-min Maxell UR cassettes to ensure all frequencies were reliably reproduced. We used Avisoft SASLab Pro to conduct acoustic analysis and the creation of sonograms of all the alarm calls recorded. With the digital conversion sampling rate set to 5500 Hz, we used a Hamming evaluation window to display and analyze calls. The upper and lower frequencies of alarm calls varied between 473 and 3445 Hz and were within the range faithfully recorded by digital storage and playback devices (Magnusson 2006). We edited vocalizations of a single wild *Ateles fusciceps* to 1-min duration, then transferred it to a digital Alba MP3 player connected to a field amplifier and speaker system (Saul Mineroff SME-AFS, Mineroff Electronics Inc., New York). We calibrated the playback system to a *ca.* 200-m radius based on human hearing range within the forest.

In the forest under investigation, we conducted field surveys during the day (0900–1700 h), walking 4–6 km/d, depending on access to area and terrain. We walked existing trails and transects with ≥3 people at 1–1.5 km/h to avoid disturbing primates. Every 500 m we played the standardized recorded vocalization for 1 min, turning every 15 s to broadcast to the 4 points of the compass. We waited for 15 min at each point to record any responses to the stimulus, a time period consistent with studies on *Ateles geoffroyi* (Chapman *et al.* 1990). At each sampling point, we recorded latitude, longitude, and altitude via a GPS (Garmin 60CSx). Other information recorded included compass direction of call, time calling, estimated distance of responding vocalization, and visual observations of number and group composition if primates approached playback.

The survey team never repeated playback surveys at the same point within a 7-day period. We took this precaution to prevent familiarization to playback vocalizations and minimize any unnatural responses by the focal subjects. Owing to the rapid nature of the survey, we assumed primate location to be static within the survey period. We estimated density by dividing the number of responses to playback at each site by the actual area sampled by playback. At some sites, the nature of the terrain resulted in some overlap between playback sampling areas. We removed overlap when calculating total area sampled at the site. At each site we estimated minimum detection frequency by regression of density against detection frequency.

The survey team conducted the first survey at the Los Cedros Biological Reserve (00°18′19″N, 78°46′28″W), a location with a known population density (Gavilanez-Endara 2006). We then applied the playback survey method in primary forest at a range of altitudes. We surveyed primates at Santa Rosa de Naranjal (00°16′N, 78°55′ W), Leon Febres Cordero (00°20′N, 79°01″W), and Tesoura Escondida (00°35′N, 79°4′W) between July 9, 2007 and July 21, 2007 (see Fig. 4). Combining primate density and a digital elevation model based on SRTM data sets (USGS 2006a, b), we generated a map of primate density for 3 altitudinal ranges. Finally we combined information from all datasets in a gap analysis to highlight areas of unprotected forest with high primate density and under low hunting pressure to guide future conservation efforts.

Results

We classified 81% of the area under study (western limit 79°12′14.3″, eastern limit 77°56′33.9″, southern limit 0°0′0.8″, and northern limit 1°48′38.6″) using a mosaic of LANDSAT images. The LANDSAT 7 image was the most recent image with minimal cloud cover over the whole study region, and subsequent older imager was used to “plug the gaps.” The only image available with no cloud cover for a small region in the south east of the study area was from 1988. This was included as a final layer. The forest remaining after processing the LANDSAT images using species-specific criteria that is suitable for *Ateles fusciceps* is shown in Fig. 1. The potential historical distribution of the primate based on MaxEnt modeling is shown in Fig. 2. The model provides a high predictive success rate (13 of 17 localities successfully predicted as present) and a highly significant distribution model ($p<0.001$).

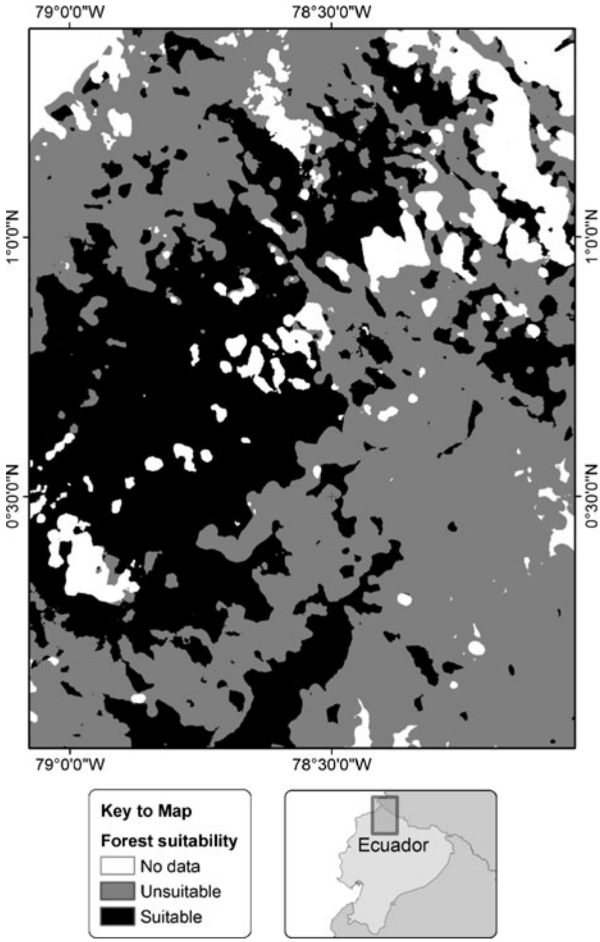

Fig. 1 Map showing forest with the potential to support *Ateles fusciceps* based on supervised classification of satellite (LANDSAT) imagery and ecological modeling (location of study area in lower right-hand box).

We clipped potential historical distribution of the primate (Fig. 2) by remaining forest capable of maintaining *Ateles fusciceps* (Fig. 1) to predict current distribution (Fig. 3). The model predicts remaining forest area capable of sustaining *Ateles fusciceps* at 5872 km^2, of which protected areas provide legal protection for 2172 km^2. Unprotected forests capable of maintaining *Ateles fusciceps* cover an area of 3700 km^2. Based on hunting buffers of 9-km radius for lowland settlements and 3-km radius for highland settlements (Fig. 4), a forested area of 2711 km^2, suitable for *Ateles fusciceps*, is impacted by high levels of hunting (Fig. 5). Of particular interest, an area of 989 km^2 of unprotected forest is suitable for *Ateles fusciceps* and is still relatively isolated from human populations and hunting pressure. The area of unprotected forest under low hunting pressure is reduced to 508 km^2 and 249 km^2 for hunting buffers of 4.5 km/13.5 km (highland/lowland settlements) and 6 km/18 km (highland/lowland settlements), respectively.

Playback field survey results show that minimum detectable density varies with effective replicate number, ranging from 0.23 to 0.68 individuals/km^2. With the exception of Leon Febres Cordero, where hunting levels were thought to be high, we observed higher densities of primates at lower altitude (Table III). Based on field

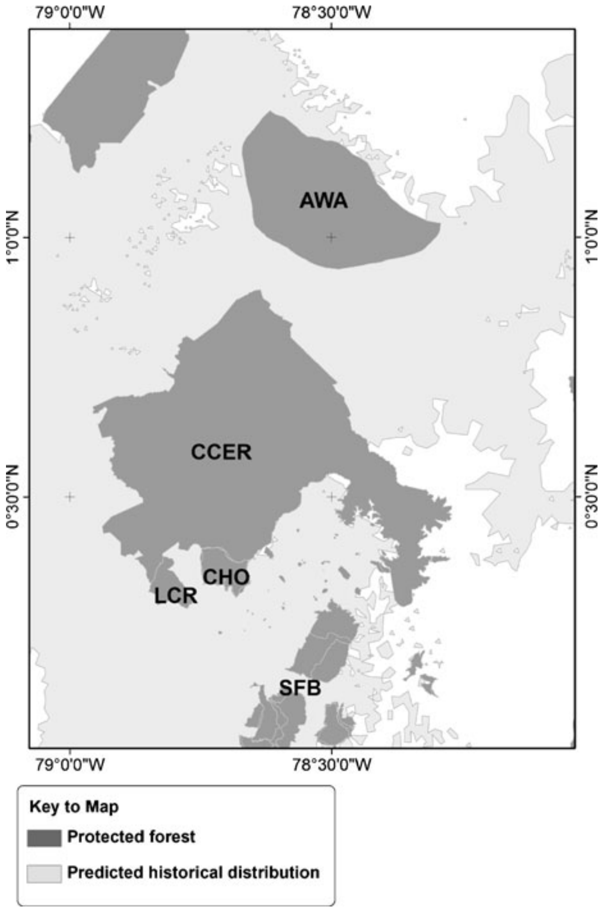

Fig. 2 Map showing MaxEnt model of potential historical distribution of *Ateles fusciceps* and existing protected areas. AWA = Awa Indigenous Reserve; CCER = Cotacachi-Cayapas Ecological Reserve; LCR = Los Cedros Reserve; CHO = Chontal Protected Reserve. SFB refers to the Southern Forest Block including protected forests of Maquipucuna, Mindo, Cambugan, Deule, and Pampolona.

survey data, we illustrate the expected densities of primates for unprotected forest under low hunting pressure within 3 altitudinal ranges (0–600 masl, 600–1200 masl, and 1200–1800 masl) (Fig. 5). Our gap analysis (Fig. 5) highlights the areas to the south and west of Cotacachi-Cayapas Ecological Reserve for conservation action. In these areas, hunting pressure is still low and population densities of *Ateles fusciceps* are highest.

Discussion

Using species-specific analyses we identified remaining forest that forms suitable habitat for *Ateles fusciceps*. A large block of continuous forest is protected within the Cotacachi Cayapas Ecological Reserve (CCER) and contiguous Los Cedros Reserve and Chontal Reserves. Other large protected forest blocks lie within the Awa indigenous reserve to the north, bordering Colombia, and forests to the south that include the protected forests of Maquipucuna, Mindo, Cambugan, Deule, and Pampolona. A large area of unprotected lowland forest lies to the west of the Cotacachi-Cayapas Ecological Reserve (Fig. 2). However, we should recognize the

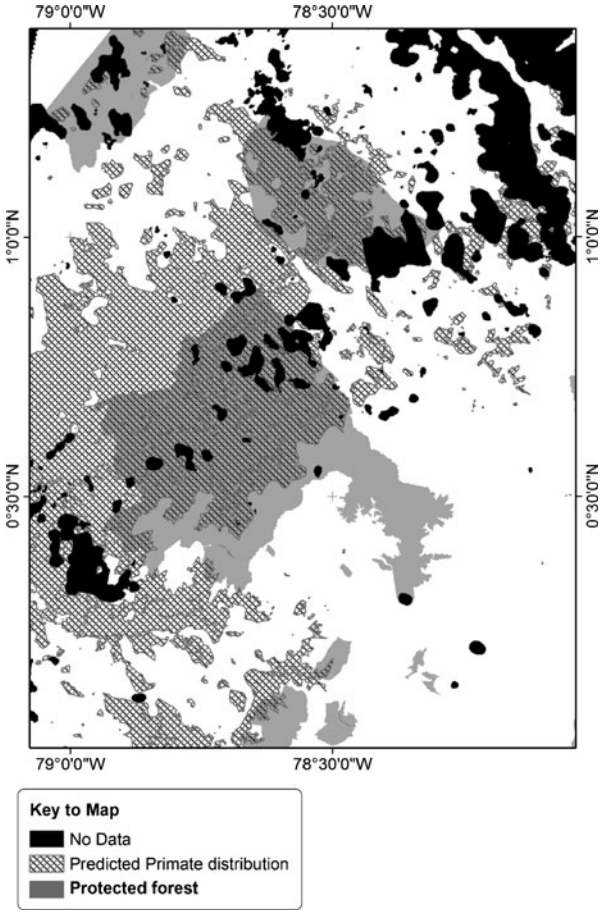

Fig. 3 Map showing remaining distribution of *Ateles fusciceps* based on the MaxEnt predictions, existing forest, and species-specific ecological criteria.

limitations of satellite image analysis in identifying forest. One of the major drawbacks of the study region, with its steep altitudinal gradients, is the near-constant level of cloud cover that makes it difficult to attain cloud-free imagery. An additional complication is a scanning fault on the LANDSAT 7 satellite since 2003 that requires users to "fill in the blanks" with archival satellite imagery. Our resulting land use classification mosaic, although based principally on 2006 imagery, is limited by the need to minimize cloud cover and address errors in the remote sensing imagery. However, the resultant image does classify >80% of the region under study. Our classification is limited by classification of forest as a single category. We were unable to subcategorize forest into primary and secondary types owing to complications associated with working in mountainous areas. This was because assigning multiple forest categories to the subtle changes in spectral signatures, associated with primary and regenerating forests, is confounded by shadows generated by the steep slopes. The data set still provides a good estimate of remaining primary forest, as the overriding process in the region is that of deforestation (Peck 2010), and other land types are clearly differentiated. There is a risk of overestimating forested area suitable for the primate because farming

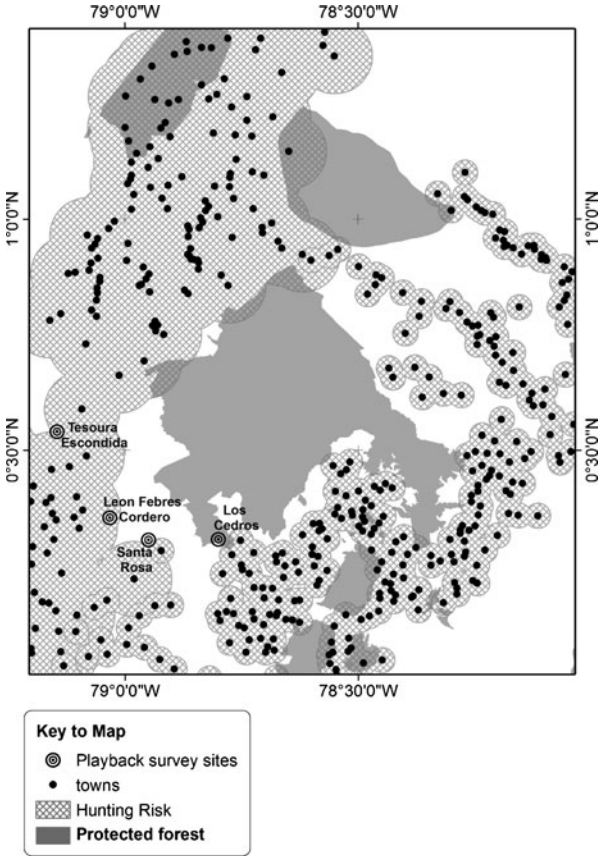

Fig. 4 Map showing hunting pressure and field survey sites. Hunting pressure is predicted based on the location of human settlements with buffers of radius 9 km applied to lowland (0–600 masl) settlements and 3-km buffers applied to highland settlements (>600 masl).

practices that generate a canopy-like structure, such as palm oil plantations and areas of secondary regrowth unsuitable for *Ateles fusciceps* (Sorensen and Fedigan 2000), could be classified as forest in this analysis.

We used a relatively low sample size for MaxEnt ecological niche modeling. As a result, the predictions of historical primate distribution represent locations of high habitat suitability for *Ateles fusciceps*, as opposed to definite species presence. However, model validation confirms that the predicted distribution is an accurate representation of actual distribution. Further, the model extends into regions where no locality data currently exist, and reveals potentially unknown populations. These areas of overprediction are useful in identifying priority areas for fieldwork, to confirm presence or absence of the study species (Thorn et al. 2009).

The acoustic playback survey method provides an estimated density of 0.9 individuals/km^2 for the Los Cedros reserve. This figure lies within the 95% confidence intervals of density estimates for *Ateles fusciceps* using line transect distance sampling (Gavilanez-Endara 2006), which reported a mean density of 1.16 individuals/km^2 (95% confidence limits of 0.48–2.81 individuals/km^2). Our density estimates for *Ateles fusciceps* are lower than those reported in the literature for other species of *Ateles* at similar altitudes, although species-specific differences may make comparison difficult (Shanee 2006). At sites with low levels of hunting we observed

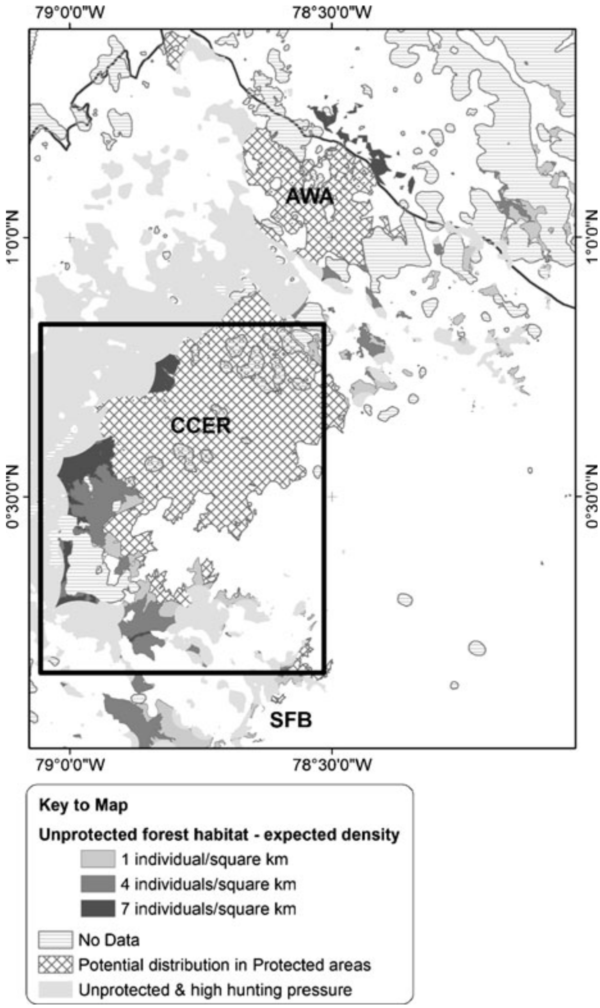

Fig. 5 Map showing predicted density of *Ateles fusciceps* in unprotected forest within 3 altitudinal ranges and recommended focus of immediate conservation action (black box).

a reduction in the density of *Ateles fusciceps* with increasing altitude. This trend is similar to that in other studies with spider monkeys and other primates. It is attributed to a reduction in fruit availability with altitude (Caldecott 1980; Durham 1975; Marshall *et al*. 2005).

It must be noted that our density estimates are all based on very low detection levels, which is inevitable when dealing with rare species that range widely. The playback methodology clearly shows potential for rapid determination of presence of *Ateles fusciceps*. It can also provide a cost- and time-effective estimate of abundance, particularly when compared to standard line transect methods. Further survey method development and field calibration are still required to address a number of uncertainties. For example, dominant individuals may be the only ones that respond to broadcast calls, resulting in an underestimate of total primate abundance using our assumptions.

Table III Estimated density of *Ateles fusciceps* with altitude based on playback field survey

Location	Effective playback sample number	Minimum detectable density (individuals/km^2)	Density estimate individuals/km^2 (observations)	Mean altitude (m)
Los Cedros Biological Reserve	34.95	0.23	0.9 (1)	1570
Santa Rosa de Naranjal	12.67	0.63	3.76 (3)	721
Leon Febres Cordero[a]	13.85	0.57	0.57[a] (1)	370
Tesoura Escondida	11.68	0.68	7.49 (3)	332

[a] Hunting activity suspected at this site

For 1 lowland site, Leon Febres Cordero, we obtained the lowest recorded density estimate of all. At this unprotected lowland site we suspect high levels of hunting, based both on our model (Fig. 4) and on personal observations at the survey site itself. During surveys we recorded a number of visual observations of *Ateles fusciceps*, but these primates did not vocalize in response to playback, remaining silent instead. This may be a response to local hunting pressure, where vocalization would alert hunters to their position. By comparison, individuals at Tesoura Escondida vocalized and actually approached the survey team. Based on conversations with local community members from Tesoura Escondida, it is clear that this area is rarely hunted. The results suggest that differences in the ratio of vocal response to visual observations without vocalization may provide an indication of disturbance pressure such as hunting. We would need to undertake further field studies to confirm whether specific primate responses and hunting pressure are actually related.

A key factor in understanding hunting patterns is access to the target prey. We predicted hunting risk by assuming hunting occurs within a circular zone surrounding human settlements. This is clearly a simplification, as it does not take into account roads, paths, and riverine transport networks as forest access points for hunters. Our model is likely to underestimate hunting activity, because even a single family can have a significant impact on primate populations (Peres 1990). Our analysis of hunting is sensitive to the size of buffers applied to settlements. Doubling the hunting radius around settlements causes a *ca.* 4-fold reduction in area of unprotected forest that remains free of hunting activity. It is clear that there is the need to better understand local hunting patterns and to address the markets, such as the pet trade, that continue to create a demand for wild primates.

Our analysis shows that 73% of unprotected forest considered suitable for *Ateles fusciceps* is deemed susceptible to hunting. It is likely that populations of *Ateles fusciceps* are already extinct or at very low levels in these areas. The remaining 26%, considered at low risk from hunters, is comprised principally of forest that buffers the southwest of the Cotacachi-Cayapas Ecological Reserve and forest within the Southern Forest Block (Fig. 5). Unfortunately, populations of *Ateles fusciceps* are no longer thought to exist within the Southern Forest Block (Diego Tirira, *pers. com.*). As a result, the boxed region in Fig. 5 is considered to be the highest priority area for conservation action. These lowland, unprotected areas, under low hunting pressure, are likely to contain high densities of *Ateles fusciceps*. This region should be the immediate focus of field surveys to confirm the existence and abundance of spider monkeys.

Protected forest covers just over 2172 km^2 of habitat suitable for *Ateles fusciceps*, across a range of altitudes. It is still unknown whether populations are present in all protected areas, owing to historical impacts or other factors. Field surveys should also include protected areas, as their capacity to restrict hunting activity effectively and preserve suitable habitat for this species is currently unknown. Urgent conservation action is now required to ensure survival of remaining populations of *Ateles fusciceps*.

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