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TEMPORAL AND SPATIAL PATTERNS OF MACAW ABUNDANCE IN THE ECUADORIAN AMAZON

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Abstract. Although macaws are arguably the most widely recognized species of bird from Neotropical rainforests, little is known of their basic biology or demography in the wild. In Ecuador, as in other Neotropical countries, it is suspected that several species of macaw are declining in response to human activity and habitat alteration but there is little hard data supporting this supposition. In this paper, we present one full year of data on macaw populations from a relatively pristine site in the Ecuadorian Amazon, and compare this site to two other sites with intermediate and relatively high levels of human activity. At Tiputini Biodiversity Station, a pristine terra-firme forest, macaws were more common in the dry season than in the wet season. This pattern is the opposite of that recently reported for seasonally inundated forests in Peru, suggesting that macaws may make large-scale, seasonal movements across habitat types. We employed the same sampling methodology for shorter periods of time at Sacha Lodge, characterized by intermediate levels of human activity, and at Jatun Sacha Biological Station, characterized by relatively high levels of human activity and habitat degradation. We recorded an intermediate number of macaws at Sacha Lodge, and the lowest densities at Jatun Sacha. Three groups of indicator taxa sampled at all three sites showed a similar pattern. These data provide a baseline for future demographic studies of macaws in the Ecuadorian Amazon and lend tentative support to the idea that macaw population declines may be linked to human activity and habitat alteration.

Key words: *Amazon,* Ara*, conservation, Ecuador, macaw,* Orthopsittaca*, Parrot.*

Patrones Temporales y Espaciales de Abundancia de Guacamayos en la Amazonía Ecuatoriana

Resumen. A pesar de que los guacamayos son en principio el grupo de especies de aves más conspicuo de los bosques neotropicales, muy poco se sabe sobre su biología básica y demografía en estado silvestre. En Ecuador, como en otros países neotropicales, se sospecha que algunas especies de guacamayos están desapareciendo en respuesta a la actividad humana y a la alteración del hábitat, aunque hay muy poca información que sustente esta suposición. En este trabajo, presentamos información sobre la demografía de los guacamayos obtenida durante un período de un año en un lugar relativamente prístino de la amazonía ecuatoriana, y lo comparamos con dos lugares que poseen niveles intermedios y altos de alteración humana. En la Estación de Biodiversidad Tiputini, un lugar con bosques de tierra firme en estado relativamente prístino, los guacamayos fueron más comunes en la temporada seca que en la temporada lluviosa. Este patrón es opuesto a lo reportado en bosques estacionalmente inundados en Perú, sugiriendo que los guacamayos podrían realizar desplazamientos estacionales a gran escala a través de diferentes tipos de hábitat. Nosotros empleamos la misma metodología de muestreo durante períodos más cortos de tiempo en Sacha Lodge, un lugar caracterizado por un nivel intermedio de impacto humano, y en la Estación Biológica Jatun Sacha, caracterizada por niveles de impacto humano y alteración de hábitat relativamente altos. Registramos un número intermedio de guacamayos en Sacha Lodge y densidades bajas en la Estación Biológica Jatun Sacha. Otros tres grupos de indicadores taxonómicos muestreados en los tres lugares visitados mostraron un patrón similar. Esta información provee una línea de base para futuros estudios demográficos de los guacamayos en la amazonía ecuatoriana y respalda de modo tentativo la idea de que la disminución de las poblaciones de guacamayos podría estar relacionada con la actividad humana y la alteración del hábitat.

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INTRODUCTION

Macaws, the largest parrots in the world, are perhaps the most widely recognized birds from the Neotropical rainforests. Many of the 16 species of macaw apparently require large tracts of relatively pristine habitat for their survival (Forshaw 1989). As such, macaws may be ideal biological indicators of rainforest conservation status. However, little systematic research on macaw ecology and abundance in the wild has been conducted to date.

Several surveys have documented temporal fluctuations in parrot populations (Saunders 1980, Smith and Moore 1992, Renton 2001), but for most species the causes and scale of these movements are not well understood. Recently, it has been reported that macaw populations fluctuate seasonally in seasonally inundated forests in the Peruvian Amazon (Renton 2002). However, without more information on macaw population trends from a range of different habitats, our understanding of their movements in the Amazon will remain fragmented at best. This lack of information, in turn, hampers important conservation measures such as reserve planning. In this paper, we present results from a one-year study of macaw abundance and diversity from terra firme forests in the Ecuadorian Amazon.

Several species of macaw are undergoing rapid population decline (BirdLife International 2000). Given our limited understanding of the basic ecology, social biology, and demography of most macaw species in the wild, it is difficult to generalize about the specific causes and the extent of these declines. Clearly, as with many large vertebrates, macaws are adversely affected by anthropogenic activities such as establishment and expansion of roads, communities, towns, and cities, collection for the pet trade or hunting, and habitat clearing, alteration, or degradation (Novarro et al. 2000, Bodmer and Lozano 2001). Throughout this paper, we use the term ‘‘human activity’’ to describe these actions, and use human population size in an area as a rough proxy for human activity. The effect of human activity on a given species of macaw's well being likely varies across species due to a complex mix of factors such as the species' ecology, fecundity, and susceptibility to collection for pet trade (Bennett and Owens 1997, Ridgley and Greenfield 2001, Snyder et al. 2002).

In the lowland Ecuadorian Amazon there are five species of macaw, four in the genus *Ara* and one in the genus *Orthopsittaca* (Ridgley and Greenfield 2001). Although none of these species are threatened globally (all five species are considered ‘‘Least Concern’’, BirdLife 2000), all are thought to have experienced different levels of population decline in Ecuador in the past 50 years, ranging from no detectable change to dramatic declines (BirdLife International 2000, Ridgley and Greenfield 2001, Ribadaneira 2002a, 2002b).

The Blue-and-yellow Macaw (*A. ararauna*) is the most common species of macaw in the Ecuadorian Amazon. Although it has declined markedly around heavily settled areas such as Tena, El Coca, and Lago Agrio, it may be the most resilient of the five species to human activity (Ridgley and Greenfield 2001). The Scarlet Macaw (*A. macao*) appears to be more sensitive. In Ecuador, the species has suffered rapid population decline in recent decades (Ridgley and Greenfield 2001) and is considered a near-threatened species (Ribadaneira 2002a). The Red-and-green Macaw (*A. chloroptera*) has undergone the most dramatic population decline of all five species, and is reported to be the most rare of the macaws in Ecuadorian Amazon (Ridgley and Greenfield 2001). This species is considered to be ‘‘Vulnerable to Extinction’’ within Ecuador (Ribadaneira 2002b). Two smaller species, the Chestnut-fronted Macaw (*A. severa*) and the Red-bellied Macaw (*O. manilata*), are locally common (Ridgley and Greenfield 2001), though the Red-bellied Macaw's apparent reliance on palm swamp habitat makes them susceptible to threats against that particular habitat (Bonadie and Bacon 2000).

The objectives of this project were two-fold. The first was to document abundance and diversity of macaws in pristine, terra firme forest (Tiputini Biodiversity Station) to improve our understanding of seasonal movements and provide a baseline for future studies. Our second objective was to compare macaw diversity and abundance at Tiputini with that of two other sites with higher levels of human activity (Sacha Lodge with intermediate human activity; Jatun Sacha Biological Station with high human activity). A map of the Ecuadorian Amazon showing the locations of sampling sites is provided in Figure 1.

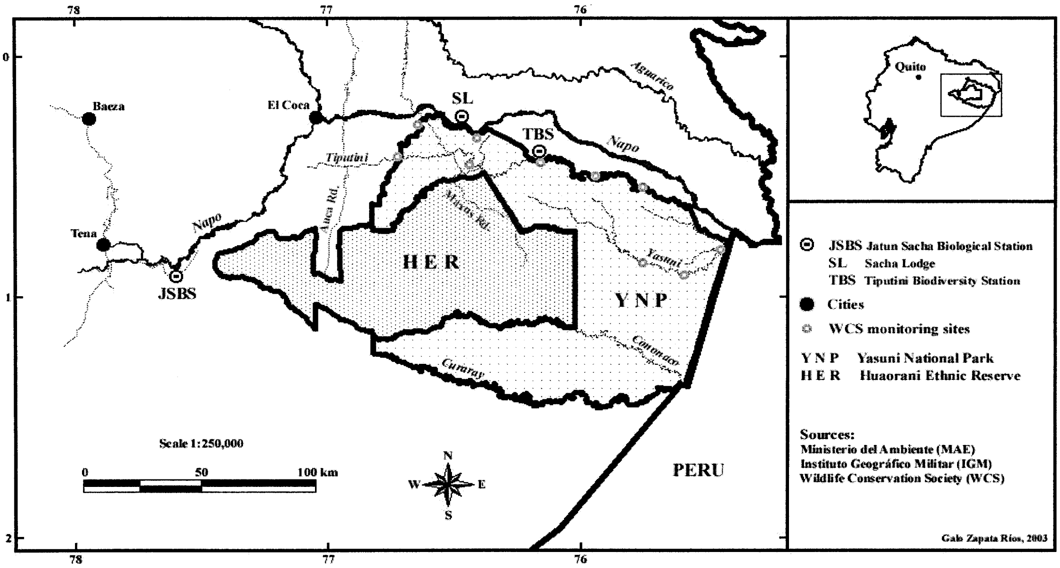

FIGURE 1. Map of the Ecuadorian Amazon with the location of each of the three study sites sampled in this study. Permission to use map granted by the Wildlife Conservation Society, Ecuador.

METHODS

SAMPLING SITES

Tiputini Biodiversity Station is situated along the Tiputini River in Orellana province, Ecuador (0°37′S, 76°10′W, 190–270 m elevation). Founded in 1994, the station covers 650 ha, virtually all of which is virgin, terra firme forest, and abuts Yasuni National Park (999 000 ha). Only staff associated with the station and the park live in the area, though there are roughly 600 field biologists and student visitors per year. The closest human settlements are small, Huaorani indigenous communities located over 20 km to the North and East, and the river in front of the station receives little traffic. Tiputini is one of the more pristine sites in the Ecuadorian Amazon.

Tiputini has marked dry and wet seasons. The dry season at Tiputini extends from October to February, with average monthly precipitation of 140 ± 21 mm per month during this 5-month period. The wet season extends from April to August, when monthly precipitation averaged 383 ± 11 mm per month. The months September and March are transition periods with intermediate levels of precipitation. Average monthly rainfall is 229 ± 24 mm per month, and the yearly average is 2.74 m per year (calcuated from Guerra 1998–2002).

Sacha Lodge is a privately run reserve located along the heavily trafficked Napo River in Sucumbios province, Ecuador (0°27′S, 76°10′W, 240-m elevation). Founded in 1990, Sacha Lodge covers 2000 ha and abuts Yasuni National Park. Sacha Lodge is primarily terra firme forest, although it also contains significant amounts of *Maruita*-dominated palm swamps and *Varzea*-dominated, seasonally inundated areas alongside the river. Sacha Lodge was our only study site that included seasonally inundated forests and substantial palm swamps. Although mostly primary forest, there are patches of secondary forest and 12 Kichwa communities within the Lodge's 2000 ha. There are more communities, and military and petroleum camps surrounding the Lodge, and the city of El Coca is 40 km to the West. The Lodge is a tourist destination with 40 cabins and a visitation rate roughly double that of Tiputini. Based on these criteria, we considered human activity in and around Sacha Lodge to be intermediate between Tiputini and Jatun Sacha. Average annual rainfall at Sacha Lodge is 2.96 m per year, with a monthly average of 247 ± 30 mm per month (Instituto Nacional de Meteorología e Hidrología del Ecuador records).

Jatun Sacha is a privately owned reserve of 2000 ha close to the Napo River, in Napo province, Ecuador (1°04′S, 77°36′W, 400 m elevation). The Reserve is roughly one-third primary, terra firme forest, and two-thirds secondary, terra firme forests in various stages of regeneration. Jatun Sacha was founded in 1985, and has an average of 1500 visitors per year, mostly volunteers who remain for one or more weeks. There are 20 communities within or immediately surrounding Jatun Sacha, and it is 500 m from a major highway, 25 km from the city of Tena, and 10 km from Puerto Misahuallí. Most of the surrounding land was cleared for agriculture and cattle, and hunting pressure around the reserve is high. Of the three sites we sampled, Jatun Sacha was influenced most heavily by human activity. Average annual rainfall at Jatun Sacha is 3.50 m per year, with a monthly average of 289 $\pm$ 16 mm per month (Instituto Nacional de Meteorología e Hidrología del Ecuador records).

We sampled macaws at Tiputini for one full year (July 2002 thru June 2003), and at Sacha Lodge and Jatun Sacha for two, 1-week periods each. Data at Tiputini were collected primarily by JF, whereas DY took data at Sacha Lodge and Jatun Sacha. Prior to beginning the formal sampling period, JF, DY, and JK spent one week together at Tiputini simultaneously but independently practicing methodologies to ensure that there were no qualitative differences in our results.

DATA COLLECTION

River transects. Each of the sites we sampled was near a large river. We conducted sampling transects along these rivers from 06:00–09:00 and 15:00–18:00, thought to represent peak activity for macaws (Gilardi and Munn 1998). We conducted surveys by floating down-river or up-river for 180 min in a motorized canoe moving at a rate equal to the flow of the river (5 km per hr, measured by hand-held GPS). We began these 15-km sampling transects either 7.5 km up-river or down-river from the station. This allowed us to use the station as the mid-point of the sampling transect without sampling the same stretch of river twice during a survey, reducing the chances of counting the same individual macaws twice within a given survey. At Sacha Lodge and Jatun Sacha, river transects were half as long as at Tiputini—they lasted 90 min and covered roughly 7.5 km—with the lodge or station as the midpoint of the transect. When a macaw was observed, we recorded: species, time of day, weather conditions, our location, bearing to the macaws, group size, and direction of flight. When macaws were heard but not seen, we recorded species when identification by vocalization was possible, and recorded group size as one individual (Renton 2002).

Tower observations. We complemented river surveys with canopy-level observations from towers. We conducted tower observations from 06:00–09:00 and 15:00–18:00 (Gilardi and Munn 1998), taking the same data on macaws as in the river surveys. We estimate that from the towers we could distinguish individual macaws at a distance of up to 300 m, and that we could see or hear macaw groups flying over the canopy up to 2000 m away. We did not differentiate between birds flying over the canopy and birds within the canopy. We omitted from analysis any groups of macaws or indicator taxa that we had already recorded during that sampling period to avoid psuedoreplication. Most flocks were easily distinguished based on flight direction and flock size (Gilardi and Munn 1998), and the relatively short sampling period (180 min) reduced the likelihood that we would count the same individuals twice in a given sampling period.

Indicator taxa. We sampled three groups of potential indicator taxa—primates (Cebidae and Callitrichidae), guans, currasows, and chachalacas (Cracidae), and toucans and allies (Ramphastidae)—at each of the study sites from November 2002 through July 2003. Primates and cracids have been shown to serve as indicator taxa in previous studies (Mittermeier 1991, Silva and Strahl 1991). Although toucans are likely more resilient to habitat degradation, they are also large vertebrates susceptible to hunting and collection for the pet trade. Encounter rates for indicator taxa were recorded from towers, but not from river transects, using the same methods described above. We estimate that we could distinguish individual primates at a distance of 100m, and we could distinguish individual cracids and toucans at a distance of 200 m (vocalizations audible up to 300 m).

SITE-SPECIFIC SAMPLING

Tiputini. We conducted regular sampling periods between 3 July 2002 and 13 June 2003 at Tiputini. Transects along rivers were conducted from November 2002 to June 2003; with 4–6 sampling trips in each of these eight months. River sampling trips at Tiputini averaged 171.6

± 0.7 min. Tiputini has two observation towers, both of which are situated in primary, terra firme forest at a height of 40 m in the crowns of emergent *Ceiba pentandra* trees. The towers are located roughly 350 m and 900 m from the Tiputini River. We sampled macaws for 53 and 41 observation periods from each of the two towers, respectively, with 3–10 observation periods per month from each tower during the study period. Each observation period lasted an average of 172.3 ± 2.1 min, and the number of observation periods from each tower was similar or identical in each month.

Sacha Lodge. We sampled Sacha Lodge on two different occasions, from 25 February 2003 to 2 March 2003, and 9–14 September 2003, for a total of 12 days of sampling. We conducted eight sampling trips on the Rio Napo (four in each visit), with trips lasting an average of 91 ± 2.5 min. We sampled macaws from two observation towers at Sacha Lodge, both in primary, terra firme forest. One tower was located roughly 1000 m straight-line from the river, and had a height of 40 m with an unobstructed view. The other tower was roughly 1200 m straight-line from the river, with a height of 48 m and the view to the north partially obstructed by the crown of another tree. We conducted 10 sampling periods at the 40-m high tower and only three at the 48-m high tower, which was built between our two visits to the lodge. Each of the observation periods at the two towers lasted exactly 180 ± 0 min.

Jatun Sacha. We also sampled Jatun Sacha on two separate occasions; from 15–20 April 2003 and 1–6 July 2003, for a total of 12 days of sampling. We sampled the Napo River ten times, and the average duration of each river transect was 89 ± 1.2 min. Jatun Sacha has one tower in primary, terra firme forest (but only 150 m from secondary forest) located roughly 1200 m straight-line from the river. The tower is 37 m above the forest floor and emerges from the canopy to provide an unobstructed, 360° view. We conducted 14 sampling periods from this tower, each exactly 180 min.

STATISTICAL ANALYSES

When analyzed independently, data from tower and river sampling sessions yielded qualitatively similar results from each site for both macaws and indicator taxa. For this reason, we chose to combine data from river and tower sampling sessions from each site for many subsequent analyses. Time of day and climate had no effect on encounter rate, so we did not control for these factors in our analyses.

Because our data were not normally distributed even after log transformations, we employed nonparametric statistical methods for comparative analyses. We used Mann-Whitney *U*-tests for pairwise comparisons (i.e., for comparisons of encounter rates from rivers and towers within each site and in relation to season; comparisons of overall encounter rates between sites and in relation to season, comparisons of average group sizes of different macaw species and of group size in relation to season, and comparisons of encounter rates of indicator taxa between sites). For comparisons including three independent variables, we used Kruskal-Wallis tests (e.g., when comparing all three sites simultaneously for variation in macaw or indicator taxa encounter rates). We accepted significance when $P \leq 0.05$ and made Bonferroni adjustments in cases of multiple, simultaneous tests. Statistical analyses were conducted using SAS V.8 software (SAS Institute 2000) and we present values as means ± SE.

RESULTS

We conducted a total of 175 sampling periods from 3 July 2002 through 14 September 2003. Of these, 129 sampling periods were conducted at Tiputini (37 river transect, 92 observation tower). Samples from Tiputini were evenly distributed between dry season ($n = 56$ observation periods) and rainy season ($n = 57$ observation periods). An additional 22 sampling periods were conducted at Sacha Lodge (8 river transect, 14 tower observation) and 24 were conducted at Jatun Sacha (10 river transect, 14 tower observation). The overall rate of encounter from all three sites was 1.4 ± 0.1 macaws hr^{-1}, with no significant variation between encounter rates from towers and rivers (Table 1).

TIPUTINI

We recorded an average of 1.8 ± 0.1 macaws hr^{-1} at Tiputini (Table 1). The encounter rate for Scarlet Macaws was twice that of Blue-and-yellow Macaws or Chestnut-fronted Macaws, and four times that of Red-and-green Macaws (Fig. 2a, b). The Red-bellied Macaw was opportunistically observed once outside of official sampling periods.

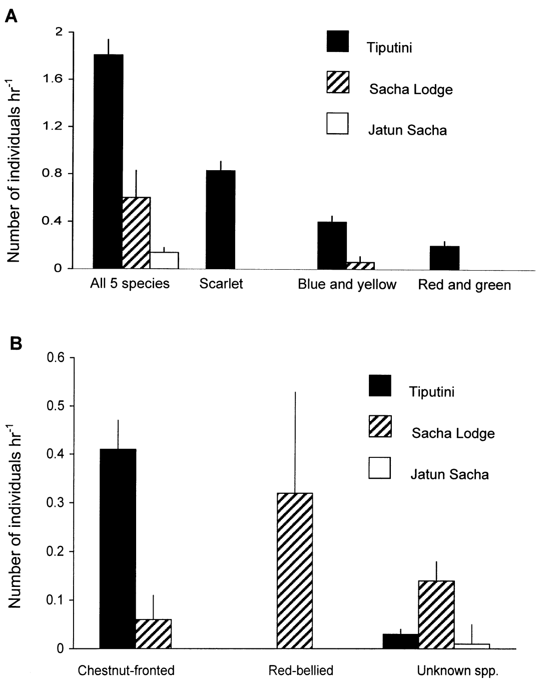

FIGURE 2. Encounter rates (mean ± SE) of A) large and B) small macaws from three sites in the Ecuadorian Amazon. Note that the scales on the X-axes differ.

At Tiputini, macaws were recorded at a higher rate during the dry season than during the rainy season, and this difference was statistically significant even after Bonferroni corrections for multiple tests (Table 2). However, no individual macaw species showed significant variation in abundance in relation to season (Table 2).

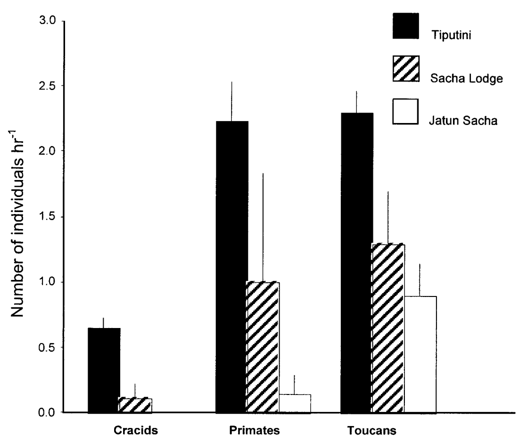

FIGURE 3. Encounter rate (mean ± SE) of indicator taxa at three sites in the Ecuadorian Amazon.

TABLE 1. Comparisons of encounter rates (individuals hr^{-1}) of macaws using two sampling methodologies (river transects and tower observations) at three sites in the Ecuadorian Amazon, and comparisons between sites for combined data (river and tower observations). Encounter rates are presented as means ± SE with the number of sampling periods at each site in parentheses.

Site	Encounter rate			Method comparison	Site comparisons	
	River	Tower	Total	River vs. Tower	vs. Tiputini	vs. Sacha
Tiputini	1.6 ± 0.2 (37)	1.9 ± 0.2 (92)	1.8 ± 0.1 (129)	$U_{127} = 2287$ $P = 0.5$	–	$U_{149} = 823$ $P < 0.001$
Sacha Lodge	0.4 ± 0.3 (8)	0.7 ± 0.4 (14)	0.6 ± 0.2 (22)	$U_{20} = 0.88$ $P = 0.8$	–	–
Jatun Sacha	0.03 ± 0.03 (10)	0 (14)	0.01 ± 0.02 (24)	NO TEST	$U_{151} = 515$ $P < 0.001$	$U_{44} = 617$ $P < 0.01$
Total	1.1 ± 0.2 (55)	1.5 ± 0.1 (20)	1.4 ± 0.1 (175)	$U_{173} = 4441$ $P = 0.2$	–	–

TABLE 2. Comparisons of encounter rates (mean ± SE) for four species of macaw in the dry season and wet season of 2002–2003 at Tiputini Biological Station, in the Ecuadorian Amazon.

Species	Encounter rate (individuals hr^{-1}) Rainy season (April–August)	Dry season (October–February)	Mann-Whitney U comparison
Scarlet Macaw	0.7 ± 0.1	1.0 ± 0.1	$U_{127} = 1299$ $P = 0.08$
Blue-and-yellow Macaw	0.4 ± 0.1	0.3 ± 0.1	$U_{127} = 1566$ $P = 0.8$
Red-and-green Macaw	0.1 ± 0.03	0.3 ± 0.1	$U_{127} = 1393$ $P = 0.1$
Chestnut-fronted Macaw	0.4 ± 0.1	0.5 ± 0.1	$U_{127} = 1289$ $P = 0.04$
All macaws	1.5 ± 0.2	2.1 ± 0.2	$U_{127} = 1140$ $P < 0.01$

We recorded no difference in macaw encounter rates from river transects and tower observation periods at Tiputini over the twelve months of this study (Table 1). Similarly, there was no difference between encounter rates from the river and towers within the rainy season (1.1 ± 0.2 vs. 1.7 ± 0.2 macaws hr^{-1}, respectively; $U_{127} = 271$, $P = 0.2$) or within the dry season (2.2 ± 0.2 vs. 2.1 ± 0.3 macaws hr^{-1}, respectively; $U_{127} = 294$, $P = 0.5$).

Average group size for all macaw species combined was 2.6 ± 0.2 individuals. There was no variation in group size between species, nor was there difference in average group size between wet and dry season within any species ($P > 0.1$ for all Mann-Whitney *U*-tests).

DIVERSITY AND ABUNDANCE IN RELATION TO HUMAN ACTIVITY

Among sites, we found significant differences in encounter rates ($H = 59.4$, df = 2, $P < 0.001$; Table 1) and in number of macaw species (Fig. 2a, b). At Sacha Lodge, a site with intermediate levels of human activity, we observed three macaw species and recorded encounter rates significantly lower than at Tiputini (Table 1). The one exception to this pattern was the Red-bellied Macaw, which was the most common species at Sacha Lodge but was not officially recorded at Tiputini. At Jatun Sacha, a site with relatively high levels of human activity, we did not positively identify any macaw species during sampling periods but one unidentified macaw was heard calling during a river transect. When we analyzed only those sampling sessions from Tiputini that coincided temporally with those from Sacha Lodge and Jatun Sacha, we found the same qualitative pattern as presented above (Table 3).

INDICATOR TAXA

Encounter rates of cracids ($H_2 = 43.0$, $P < 0.001$), primates ($H_2 = 24.0$, $P < 0.001$), and toucans ($H_2 = 26.5$, $P < 0.001$) varied significantly between the three sites, even after Bonferroni adjustments were made (adjusted *P*-value = 0.02). We recorded the highest encounter rates

TABLE 3. Results of contemporaneous sampling of macaws in pristine forest (Tiputini Biodiversity Station) and relatively degraded forests (Sacha Lodge and Jatun Sacha) in the Ecuadorian Amazon.

Period of year	Encounter rate (individuals hr^{-1}) Pristine forest	Degraded forest	Mann-Whitney U comparison
April	2.4 ± 0.4	0[a]	No Test
February–March	2.3 ± 0.5	0.2 ± 0.13[b]	$U_{41} = 107$, $P < 0.01$
July	1.4 ± 0.8	0.03 ± 0.03[a]	$U_{16} = 87$, $P < 0.01$
September	1.7 ± 0.3	0.4 ± 0.2[b]	$U_{16} = 81$, $P = 0.03$

[a] Jatun Sacha study site.
[b] Sacha Lodge study site.

at Tiputini, intermediate rates at Sacha Lodge, and lowest encounter rates at Jatun Sacha (Fig. 3). In pairwise comparisons, encounter rates at Tiputini were significantly higher than those at Sacha Lodge for cracids (U_{118} = 705, $P < 0.01$), primates (U_{115} = 801, $P < 0.01$), and toucans (U_{118} = 921, $P < 0.01$), even after making a Bonferroni adjustment for multiple tests (adjusted P-value = 0.02). Similarly, we recorded significantly higher encounter rates at Tiputini than at Jatun Sacha for cracids (U_{120} = 720, $P < 0.01$), primates (U_{120} = 840, $P < 0.01$), and toucans (U_{120} = 730, $P < 0.01$), even after making a Bonferroni adjustment for multiple tests (adjusted P-value = 0.02). As was the case with macaws, a qualitatively similar pattern was found when results from Jatun Sacha and Sacha Lodge were compared to the subset of data from Tiputini that coincided temporally with those sampling trips. Differences between Sacha Lodge and Jatun Sacha were not statistically significant for any of the potential indicator taxa ($P > 0.2$ for all).

DISCUSSION

Macaw abundance was higher in the dry season than in the wet season at Tiputini. A recent survey (Renton 2002) reports the opposite pattern for Scarlet and Red-and-green Macaws in the Peruvian Amazon, where the birds were less common in the dry season (defined as July to September) than in the wet season (January to April). Whereas Tiputini is terra firme forest with no floodplains in the immediate vicinity, the study in Peru was conducted in seasonally inundated forest. It is possible that these habitat differences have resulted in the ''mirror image'' differences between the two sites, and that the seasonal fluctuations we observed in macaw numbers in the terra firme forests of Tiputini are the counterpart of opposite trends in seasonally inundated forests like those studied by Renton (2002).

The causes underlying the seasonal movements presented here and in Renton (2002) are unclear. Renton (2002) suggested that macaws might be using inundated forests for breeding in the wet season. In keeping with this idea we saw no breeding behavior in Tiputini's terra firme forest in the dry season when the birds were most common, but did record a low level of cavity exploration in the wet season when birds were least common (n = 3 cases). It is also likely that seasonal movements are used to track fruit production in different habitat types over the course of the year. Better data on macaw breeding biology, habitat characteristics, and the timing of fruit production would allow more detailed investigation into the causes underlying macaw movements. Regardless of the underlying causes, however, the combined message from this and Renton's (2002) study is that large-scale movements by macaws are potentially very important, and that they must be understood before conclusions can be reached about the abundance and conservation status of macaws in the Amazon. Satellite tracking is one plausible approach to obtain these data.

While the Scarlet and Red-and-green Macaws showed seasonal variation in both this study and in Renton (2002), the Blue-and-yellow Macaw did not vary in relation to season in either of the studies. This suggests that Blue-and-yellow Macaws may have some important behavioral or ecological differences from the other two large macaw species. As with an earlier study of macaws in Peru (Gilardi and Munn 1998), we found that group size did not vary among species or seasonally.

The establishment of baseline quantitative data from Tiputini, one of the few remaining pristine sites in the Ecuadorian Amazon, may provide an important reference point for future studies of macaw population trends. The problem of ''shifting baselines'' is recognized as one of the greatest challenges facing researchers attempting to chart long-term population trends. In this study we have used repeatable methods to survey macaws and indicator taxa for one full year with the aim of facilitating future studies designed to document long-term population trends. Tiputini is currently considered one of the more pristine sites in the Ecuadorian Amazon, but human activity is increasingly encroaching upon the site, most immediately in the form of geoseismic surveys for petroleum.

Different sampling methods of parrots may bias results in different directions (Casagrande and Beissinger 1997). Ours is one of the few studies to sample multiple sites from towers, as well as from rivers, and we found no variation in the two sampling methodologies. While tower observations are not available at many sites, we follow Gilardi and Munn (1998) in suggesting canopy-level observations as a reliable method of sampling macaws when possible.

The three sites we sampled in this study all contained primary, Amazonian rainforest, but they varied in habitat quality and degree of human activity: Tiputini was relatively pristine, Sacha Lodge was intermediate, and Jatun Sacha had the most degraded forests and the highest level of human activity. We found that macaw abundance and diversity declined with increased human activity and habitat degradation. However, several limitations of this aspect of the study should be noted before continuing with a discussion of results. The first limitation is that our sampling effort at Sacha Lodge and Jatun Sacha was less than the full year of data we recorded at Tiputini. Since we found seasonal variation in macaw abundance at Tiputini, it is possible that we sampled Sacha Lodge and Jatun Sacha at times of relatively low abundance, leading to underestimates of the number of macaws in the area. We attempted to correct for this imbalance in sampling effort by conducting separate analyses in which we compared only the data from Tiputini that coincided temporally with data from Sacha Lodge and Jatun Sacha, and found no differences. Also, since Sacha Lodge is relatively close to Tiputini (the two sites are separated by about 25 km) it is unlikely that Sacha Lodge would experience different seasonal regimes.

We sampled only three sites in this study; too small a sample size to allow definite conclusions about the relationship between human activity and macaw abundance and diversity. A next clear step understanding the relationship between the two is to sample more sites. Another step is to quantify levels of human activity and other parameters of habitat quality with more accuracy, preferably with GIS imaging.

Finally, it may be possible that differences in habitat type may better explain variation in macaw abundance and diversity than anthropogenic activity. This seems unlikely for Sacha Lodge and Tiputini, as the two are relatively close together, and at a similar elevation in terra firme forest. Sacha Lodge, however, contains much more palm swamp habitat than does Tiputini. This likely explains the fact that Red-bellied Macaws, which rely on palm swamp habitat (Bonadie and Bacon 2000), were the only species more common at Sacha Lodge than at Tiputini. Jatun Sacha is at a higher elevation and relatively far from the other two sites but remains within the elevation and geographical range of all the species under study. Although we found very few macaws at Jatun Sacha, they were present in the site historically, and there are many reports of macaw declines at Jatun Sacha in recent years (e.g., B. Bochan in Ridgley and Greenfield 2001).

While we recognize the short-comings of this study, we do consider it meaningful that overall macaw encounter rate and number of species were negatively related to our indices of human activity. This pattern was robust between the three sites, even when timing of sampling effort was controlled. Three groups of potential indicator taxa followed this same pattern, suggesting a larger pattern of reduced diversity in relation to increased human activity. To the best of our knowledge, this study represents the first attempt to systematically compare macaw abundance and diversity in multiple sites that vary in degree of human activity. As stated above, however, a larger number of sites and more quantitative measures of habitat type and human activity are needed before firm conclusions can be reached.

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