

Edge Effects in the Primate Community of the Biological Dynamics of Forest Fragments Project, Amazonas, Brazil

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ABSTRACT While much is known about abiotic and vegetative edge effects in tropical forests, considerably less is known about the impact of forest edges on large mammals. In this study, we examine edge effects in a primate community to determine: 1) the distance from the edge over which edge effects in primate density are detectable, 2) whether individual species exhibit edge effects in their density, and 3) whether biological characteristics can be used to predict primate presence in edge habitats. Given their importance to many primate species, we also examine the influence of the number of large trees. We found edge penetration distances of 150 m for the five species that experienced edge effects, suggesting that primates respond to edge-related changes in the plant community that are known to be strongest over the first 150 m. Four species had higher edge densities:

Alouatta macconnelli (folivore-frugivore), *Chiropotes chiropotes* (frugivorous seed predator), *Saguinus midas* (frugivore-faunivore), and *Sapajus apella apella* (frugivore-faunivore); one species' density was lower: *Ateles paniscus* (frugivore); and the final species, *Pithecia chrysocephala* (frugivorous seed predator), did not show an edge-related pattern. The lone significant relationship between the biological characteristics examined (body weight, diet, group size, and home range size) and primate presence in edge habitats was a negative relationship with the amount of fruit consumed. Though we did not examine primate responses to edges that border a denuded matrix, we have shown that edges influence primate distribution even following decades of secondary forest regeneration at habitat edges. *Am J Phys Anthropol* 155:436–446, 2014. © 2014 Wiley Periodicals, Inc.

The term “edge effect” traditionally refers to an increase in the number of species where two habitats intergrade. However, today it generally describes the “changes occurring in previously undisturbed forest by the abrupt creation of a very sharp edge at a reserve margin” (Lovejoy et al., 1986, p. 258). Large-scale forest edges are generally anthropogenic creations that follow forest clearance for activities like ranching, farming, logging, and road construction. Understanding the effects of anthropogenic edges is important because edges are widespread features that may, among other things, create ecological traps (Lehman et al., 2006a), alter food availability (Lehman et al., 2006b), or lead to increased parasite loads (Chapman et al., 2006). Indeed, 50,000 km of new forest edge is created each year in the Brazilian Amazon alone (Broadbent et al., 2008). As a result, a species' ability to utilize edges will influence their ability to survive in the face of continuing forest conversion.

Primatological studies that systematically test for edge effects and the distance from the edge over which they are detectable (edge penetration) are uncommon; indeed, the only published research has focused on lemurs. Two of these studies systematically examined edge penetration depths, detecting edge responses over the first 300 m for many species and over the first 600 m for a few others (some species showed no edge response) (Lehman et al., 2006a,b). The relationship

between primate density and distance to the edge can take three forms. As proximity to the edge increases, density can: 1) increase (a positive edge effect), 2) decrease (a negative edge effect), or 3) show no edge-related pattern (a neutral edge effect) (Reis et al., 2004). Two types of lemurs appear to exhibit negative edge effects: 1) highly frugivorous species, due to edge-related increases in the mortality of large fruiting trees (Lehman et al., 2006a; Lehman, 2007), and 2) species that rely on torpor, which can be inhibited by edge-related temperature increases (Lehman et al., 2006c). Positive edge effects have been attributed to diet, with species exhibiting diverse diets thriving at the intersection of multiple habitats (Lehman et al., 2006c), as well as to

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increased food abundance (arthropods: Lehman et al., 2006b,c; food trees: Lehman et al., 2006b; foliage and/or leaf nutrient content: Lehman et al., 2006b). Lastly, species that exhibit neutral edge responses have been either: 1) folivores whose food trees may not experience edge-related changes (Lehman et al., 2006c; Lehman, 2007), 2) bamboo specialists (Lehman et al., 2006c), or 3) frugivores that have been studied in the dry season when their diets contained significant foliage (Lehman et al., 2006b,c; Quéméré et al., 2010).

Lemur responses to edge habitats can be used to formulate predictions about the ways in which anthropoid primates will respond to forest edges. Of additional use in formulating predictions are primate responses to selective logging where individual treefalls and logging paths create numerous localized edges. Among Neotropical primates, large frugivores decline in response to logging while species that consume significant amounts of foliage and arthropods may be successful (Johns and Skorupa, 1987). Overall, many species of primates persist in logged habitats provided that the disturbance is not severe, not accompanied by strong hunting pressure, and that it does not selectively remove trees that are important sources of food (Johns and Skorupa, 1987).

In general, large-bodied, heavily frugivorous primates that rely on the fruit of large mature forest trees (e.g., *Ateles*: van Roosmalen, 1985) should exhibit negative edge effects (Lehman et al., 2006a; Lehman, 2007) because large tree mortality increases at habitat edges (Kapos et al., 1993; Laurance et al., 2000) and these primates may not utilize the small, sugary, and nutrient poor fruits that often characterize the secondary tree species that colonize treefall gaps (Grieser Johns 1997). Primates with varied diets, in contrast, will be attracted to habitat edges because they are the intersection of multiple habitats with disparate floral and faunal communities (Lehman et al., 2006c). Edges will be especially appealing to faunivorous species due to elevated arthropod abundance (Fowler et al., 1993; Malcolm, 1997). Folivores will exhibit positive, or perhaps neutral, edge effects because edges have: 1) abundant pioneer trees whose leaves contain weak chemical defenses, and 2) mature forest species with more abundant young, poorly defended leaves (Coley, 1980; Chen et al., 1992; Williams-Linera, 1990) in addition to leaves with higher protein concentrations (Ganzhorn, 1995). Body size may also be important because edge-related damage to the tree community can lead to broken canopies with frequent gaps and dense understories (Laurance, 1991; Camargo 1993; Camargo and Kapos, 1995), a pattern that we hypothesize will discourage edge use by large arboreal species but encourage it in smaller species. While this hypothesis will not find support in a study of recent gaps that lack pioneer trees and therefore also pose barriers to smaller species, we hypothesize that older gaps filled by dense stands of pioneer trees may have extensive subcanopy pathways that facilitate the movement of small and medium primates while doing little to lessen the disruption of the canopy pathways used by larger species.

Research was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), an experimental, landscape-level project designed to examine the minimum habitat fragment size necessary to maintain the biodiversity of an undisturbed primary forest. The fragments were isolated in the middle of cattle ranches following clearcuts in the early 1980s; the ranches

themselves are surrounded by large expanses of undisturbed primary forest. The edge sampled in this study is the boundary between primary forest and 19–30-year-old secondary forests regenerating on abandoned, clearcut cattle pastures. As a result, many of the microclimatic edge effects that follow edge creation are likely reduced or absent due to the edge-related proliferation of vines and secondary growth (Camargo and Kapos, 1995; Didham and Lawton, 1999). However, edge effects like desiccation stress, wind shear, and wind turbulence have long-term impacts because they increase tree mortality and damage (Laurance et al., 1997, 1998), especially in large trees (Laurance et al., 2000), and significantly alter the composition of the mature tree (Laurance et al., 2000, 2006) and liana communities (Laurance et al., 2001). These effects are long-lasting and do not disappear with edge closure. Indeed, they may grow in severity after exposed edges are filled by the growth of new vegetation (Laurance et al., 2011) because the force of the winds acting on mature forest trees in edge habitats increases following edge closure (Somerville, 1980; Savill, 1983; Reville et al., 1990).

In this study, we examine edge effects at the boundary between the BDFFP's now-abandoned cattle pastures and the surrounding primary forest and consider two questions. The first question has two parts: 1a) what is the magnitude of edge penetration in terms of primate density, and 1b) which of the primates of BDFFP show edge effects in their population densities? The majority of strong edge effects penetrate less than 150 m into remnant forests in the tropics (Laurance, 2000), and as a result we expect to see primate edge responses over this same area. The magnitude of the strongest edge-related changes in the plant community [e.g., canopy height: 100 m (Camargo, 1993), canopy damage: 150 m (Laurance, 1991), elevated frequency of treefall gaps: 160–190 m (Wandelli, 1991; Kapos et al., 1993), and large tree mortality: 300 m (Laurance et al., 2000)] should approximate the depth to which primates are able to perceive, and respond to, edge effects given that plants, especially trees, provide primates with food, substrates for locomotion, habitat for prey, sleeping sites, and protection from predators.

For individual species we predict: 1) positive edge effects for howler monkeys (*Alouatta macconnelli*) due to their highly folivorous diets (Table 1), and white-faced sakis (*Pithecia chrysocephala*) due to their use of understory in areas with edge-like habitats (Schwarzkopf and Rylands, 1989; Walker, 1996); 2) a negative edge response for the large-bodied, highly frugivorous spider monkey (*Ateles paniscus*) (Table 1); and 3) neutral edge responses for brown capuchins (*Sapajus apella apella*) and golden-handed tamarins (*Saguinus midas*). Although these species have small-to-medium body sizes and faunivorous–frugivorous diets that suggest positive edge effects, we expect neutral edge effects because both species heavily utilize secondary growth forests like those that border the edge (Lenz, 2013) and as a result the edge will be a transitional zone between two viable habitats offering different resources (Table 1). We also predict a neutral edge response for bearded sakis (*Chiropotes chiropotes*), although we are admittedly less certain regarding their edge use. While a negative edge response might be expected given their frugivorous diet (Table 1) and preference for tall, undisturbed primary forests (Mittermeier, 1977; Ayers, 1989), bearded sakis at the study site utilize forest edges and habitat

TABLE 1. Characteristics of the primates of the BDFFP

Species*	Avg. weight (kg) ^z (♂+♀)	Avg. group size	Avg. home range (ha)	% of Diet ^{aa}			
				Fruit**	Flower	Leaf	Other
<i>Alouatta</i> ^{ab,f}	6.8	8.2 (4–17)	53 (4–166)	40.4	6.4	48.1	5.1
<i>Ateles</i> ^{g,j,k,n}	7.8	14.3 (12–18)	224 (153–255)	88.7	3.8	6.1	1.4
<i>Chiropotes</i> ^{h,r}	2.8	21.8 (8–44)	336 (200–559)	87.9	5.7	5.8	0.6
<i>Pithecia</i> ^{o,u,v,w}	1.7	3.4 (1–12)	103 (10–287)	86.4	2.1	8.7	2.8
<i>Saguinus</i> ^{i,z}	0.5	5.7 (3–8)	33 (28–43)	66.0	1.9	0.8	31.3
<i>Sapajus</i> ^{g,o,aa,ad}	2.6	14.3 (6–23)	429 (250–850)	65.0	1.4	2.7	30.9

Data range is in parentheses where relevant. (Partial reproduction with permission from [Boyle and Smith, 2010]).

*We use *Sapajus* where the Boyle and Smith (2010) used *Cebus*.

**Large portions of the diets of *Chiropotes* (74.47), *Pithecia* (43.15), and *Sapajus* (20.5) are composed of seeds.

Ford and Davis (1992).

^a Seed data are a subset of the total fruit percentage. Sources did not note seeds as dietary items for three species. "Other" consisted primarily of insects, exudates, and small vertebrates.

^b Gaulin and Gaulin (1982).

^c Julliot and Sabatier (1993).

^d Julliot (1996).

^e Palacios and Rodriguez (2001).

^f Sekulic (1982).

^g Guillotin et al. (1994).

^h Kinzey and Norconk (1990).

ⁱ Mittermeier and van Roosmalen (1981).

^j Norconk and Kinzey (1994).

^k Simmen (1992).

^l Simmen and Sabatier (1996).

^m Symington (1988).

ⁿ van Roosmalen (1985).

^o Norconk et al. (2003).

^p Ayres (1981).

^q Boyle et al. (2009).

^r van Roosmalen et al. (1981).

^s Kinzey and Norconk (1993).

^t Lehman et al. (2001).

^u Norconk (1996).

^v Oliveira et al. (1985).

^w Vié et al. (2001).

^x Day and Elwood (1999).

^y Kessler (1995).

^z Oliveira and Ferrari (2000).

^{aa} Izawa (1980).

^{ab} Peres (1993).

^{ac} Spironello (2001).

^{ad} Zhang (1995).

fragments that are heavily influenced by edge effects (Boyle et al., 2009), suggesting a potentially positive edge response.

Our second question examines whether or not biological characteristics (body weight, diet, group size, and home range size) predict primate presence in edge habitats. (Hereafter the word "presence" refers only to primate presence/absence in an edge zone over all samples; it does not refer to density.) We predict that body size will be negatively related to edge presence due to the challenges of canopy travel discussed above. We also predict a negative relationship with the percentage of fruit in the diet, which we consider as a loose proxy for dietary flexibility, with lower overall fruit consumption equating to a more flexible diet because these species consume a greater amount of nonfruit items (e.g., *Ateles* vs. *Sapajus*). In addition, we seek to determine whether species-typical home range and group sizes preclude heavy use of habitat edges because home range or group size is too large to permit concentration on narrow edge habitats. As the edges under consideration are part of large tracts of primary forest, area requirements should

not be a factor in edge use as they might be in smaller habitat fragments and we therefore do not anticipate influences from home range size or group size. As a control, we consider whether the same biological traits predict presence in the forest interior.

METHODS

Study site

The study site, the BDFFP, is located in the central Amazon 80 km north of Manaus, Brazil. The forest is tall *terra firme* rain forest with a closed canopy between 30–37 m and emergents to 55 m (Laurance et al., 1998b). We collected data at two of the project's three ranches (Dimona and Porto Alegre). Average annual rainfall during this study was 2194 mm with a dry season from June to October.

The BDFFP's primate community is composed of six species: black-bearded sakis (*Chiropotes chiropotes*) (Veiga et al., 2008), golden-faced sakis (*Pithecia chryscephala*) (Marsh, 2014), golden-handed tamarins (*Saguinus midas*) (Mittermeier et al., 2008a), Guiana spider

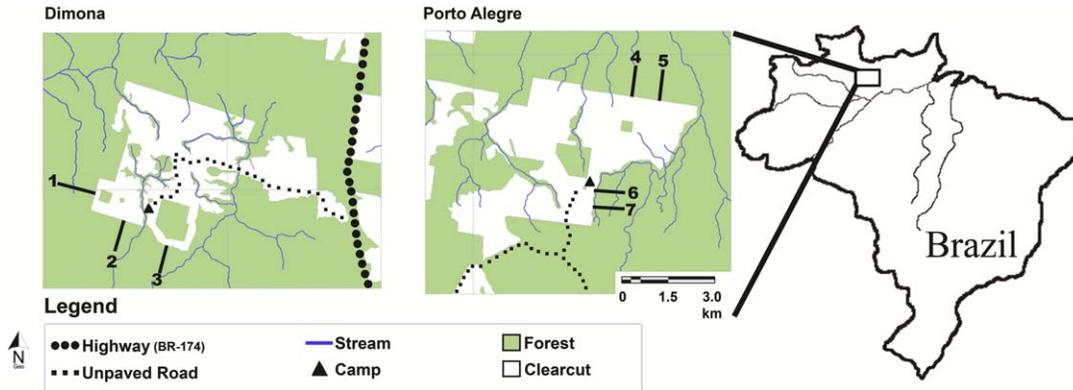


Fig. 1. The two ranches where this study was conducted, Dimona and Porto Alegre, with the locations of the seven edge transects sampled in this study. Transects 1–5 sample undisturbed primary forest and transects 6–7 sample selectively logged primary forest. (Basemap created by E.M. Venticinque and T.L.M. Fernandes and modified by the authors). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

monkeys (*Ateles paniscus*) (Mittermeier et al., 2008b), Guianan brown capuchins (*Sapajus apella apella*) (Rylands et al., 2008), and Guianan red howler monkeys (*Alouatta macconnelli*) (Boubli et al., 2008). We use the IUCN Redlist's taxonomy but place the Guianan brown capuchin in the genus *Sapajus* (Lynch Alfaro et al., 2012). Hereafter each species is referred to by genus alone.

Data collection

Between November–December 2008, June–November 2009, and January–June 2010, we conducted primate surveys for a total of 209.35 km over five unlogged primary forest transects: 1) 1.05 km (42 replicates), 2) 1.10 km (38), 3) 0.85 km (37), 4) 1.00 km (46), 5) 1.00 km (46), and a total of 118.04 km over two lightly logged primary forest transects (2 stumps/4.18 ha = 0.48 trees/ha): 1) 1.03 km (58), 2) 1.06 km (55) (Fig. 1). Two observers, 5–10 m apart and with the author (Lenz) always in the lead, walked transects slowly (average speed = 1.01 km/h). We used a Nikon Forestry 550 laser rangefinder to measure the sighting distance and height of the first individual sighted in each primate group and a Suunto MC-2G global compass to measure the sighting angle. We also recorded our location, counted the number of individuals, and estimated group spread along two perpendicular axes. We should note that the large home ranges of *Chiropotes* (300–559 ha: Boyle, 2008), *Sapajus* (852 ha: Spironello, 2001), and perhaps *Ateles* (ranging patterns yet to be examined at the BDFFP) make it possible that our transects did not allow us to obtain a substantial sample of groups whose ranges consist entirely of interior forest without access to edge habitats.

We repeatedly sampled the seven transects, each of which was perpendicular to the primary forest edge, 950–1100 m in length (Fig. 1), and ~1.0 km from the nearest other transect (range 600–1250 m) in an effort to sample as many distinct groups as possible (Sorensen and Fedigan, 2000). We sampled transects in pairs [as labeled in Fig. 1: 1 (paired with a transect not included in the present study), 2 and 3, 4 and 5, 6 and 7]. Each day was devoted to a single transect pair, with each transect in the pair sampled once in the morning and once in the afternoon. We began surveys at the end points of transects and alternated start points to avoid bias. Sam-

pling began at 06:45 and 13:15 to allow a minimum of 6.25 h between resampling, more than the 3 h suggested as a sufficient rest period. Sampling was slightly more common in the dry season (55.1%) than in the wet season (44.9%). This slight imbalance did not influence perpendicular detection distances as Mann–Whitney *U*-tests revealed an interseasonal difference for only *Pithecia*, a finding that we attribute to statistical noise in a small sample ($N = 21$) rather than a real difference given the lack of differences in interseasonal detection distances for all other species. In addition, Chapman et al. (1988) note that reduced detection probabilities at certain times will be compensated for by narrower transect widths (the authors are discussing time of day, but the point holds for potential interseasonal variation). We therefore lumped all data across seasons for all species.

We identified and measured all trees ≥ 10 cm DBH (1.3 m) to a depth of 2 m along each side of the full length of all transects. We chose a 10-cm DBH threshold because it is commonly used to characterize Amazonian tree communities (e.g., Pitman et al., 2002; Nascimento et al., 2013). The locations of individual trees were recorded in 10-m intervals using the meter numbers on our transects. This allowed us to include the number of large trees (≥ 60 cm DBH) per ha in our analyses as least two of the primate species of the BDFFP, *Alouatta* and *Ateles*, frequently utilize large trees. Identifications were done in the field by expert Paulo Apóstolo Assunção (da Ribeiro et al., 1999). We sampled a total of 2,002 ha of primary forest (1639 stems ≥ 10 cm DBH, 425 species) and 0.836 ha of secondary forest (657 stems ≥ 10 cm DBH, 282 species).

Analyses and statistics

Density is calculated as the number of individuals in a given area, in this case edge zones of 150 m and the forest interior. To determine the area sampled, we estimated species-specific transect widths using the perpendicular distance to the first individual sighted and a 50% criterion for fall-off distance with a correction for group spread, referred to hereafter as the Whitesides Method, a technique that can work well for smaller sample sizes (Whitesides et al., 1988). There are several means of estimating primate density, including using either perpendicular distance (e.g., Whitesides et al.,

1988) or animal-observer distance to calculate strip width. However, the latter should not be used because these methods are conceptually and mathematically flawed (Plumptre and Cox, 2006; Buckland et al., 2010a). Newer programs like Distance (Buckland et al., 2001) are generally preferable because they are more systematic, though they require a sufficient number of observations (60–80 sightings per species, with larger numbers needed for species with variable group sizes) and sampling design (10–20 replicate transects suggested as a minimum) (Buckland et al., 2001). While this study falls short of these ideal requirements, given its widespread use we also used the Distance program, hereafter referred to as the Distance Method, to analyze the data where the methods of Whitesides et al. (1988) found significant differences (edge of 0–150 m vs. forest interior) in an effort to determine if overall patterns were the same even if statistical significance was not.

To estimate perpendicular distances we used data from a total of eight transects, seven of which contained the habitat edges examined in this study. Individual transects sampled multiple habitats: undisturbed primary forest (five transects), selectively logged primary forest (two transects), secondary forest on unburned pastures (three transects), secondary forest on burned pastures (one transect), a 10 ha habitat fragment (one transect), and a 100-ha habitat fragment (one transect). We included data from all transects to bolster sample sizes for improved estimates of transect width. Before combining data from multiple habitats we used Kruskal–Wallis tests to look for interhabitat differences and also reclassified the forest types into two broader habitat types (secondary and mature forest) and conducted Mann–Whitney U -tests to be certain we were justified in combining these data. We also used the Mann–Whitney U -test to compare the number of large trees (≥ 60 cm DBH) in edge (0–150 m) vs. interior habitats along transects in undisturbed and selectively logged forests. We combined primate sightings from undisturbed and selectively logged primary forest in density calculations for our examination of edge effects when we found no significant differences in any of the following: 1) number of stems ≥ 10 cm DBH/ha (Mann–Whitney), 2) average DBH (independent samples t -test), and 3) the density of each primate species.

Density calculations: The Whitesides Method. We calculated the area sampled for each primate species as well as primate density following Whitesides et al. (1988) except when a transect terminus sampled the same habitat as the rest of the transect. In this case, we modified the formula for area sampled to include the half-circle sampled beyond the end of the transect (through the addition of “ $0.5 \cdot \pi \cdot \text{radius}^2$,” where radius = effective distance + $0.5 \cdot \text{group spread}$).

Density data are counts and can be modeled with generalized linear models utilizing the Poisson or negative binomial distributions, the latter of which is useful for data that have an excess of zeroes (Warton, 2005). We tested our data using both the Poisson and negative binomial distributions, using the Quasi Akaike Information Criterion (QIC) to evaluate model fit with each distribution, and found the negative binomial model produced a much better fit (i.e., lower QIC) in every instance. We therefore used repeated-measures negative binomial generalized estimating equations (GEE) with a

log link and the natural log of the area sampled as an offset, running separate models for each primate species. We also used QIC to select the appropriate correlation matrix (independent, autoregressive, exchangeable, or unstructured) and a model-based estimator because we had < 20 clusters (transects) (Garson, 2010).

To test for interhabitat density differences and edge penetration depth (in 150-m intervals), we ran a GEE, as above, with habitat as the only variable and used the least significant difference test for planned comparisons. We first tested two edge zones (0–150 and 150 m end, where the end ranged from 850 to 1100 m). When we found a significant difference, we added another 150-m increment, testing 0–150 vs. 150–300 m vs. forest interior. We continued adding 150-m zones until the interior and the zone adjacent to it were equivalent, at which time we lumped these two zones and considered them to be the forest interior. If the initial test (0–150 m vs. forest interior) found both zones to be equivalent, we considered edge effects to be neutral and did not test additional intervals. We then ran a main-effects GEE with habitat (edge vs. interior) and the number of large trees/ha, testing for multicollinearity using a variance inflation factor of 4.0; no covariates required removal. We also tested multiple coding schemes for categorical variables because dummy coding can influence multicollinearity (Wissmann et al., 2007).

Density calculations: The Distance Method. One of the difficulties in using the program Distance to estimate primate density is that it requires the use of either the perpendicular distance to the group center or measurements to each individual primate. The former can be difficult to determine in the field and measurement of the latter is often impractical (and inappropriate if the individuals move after their initial detection). A solution to these difficulties is the use of the measured/estimated group center when possible and two adjustments to data collected on the first individual sighted when reliable measurements/estimates of the group center are not possible (Buckland et al., 2010b). For the first potential adjustment, in cases where the group does not straddle the transect, perpendicular distance to the group center is estimated following Whitesides et al. (1988): measure the perpendicular distance of first individual and correct for group spread (Buckland et al., 2010b). In the second potential adjustment, when a group is located on both sides of the transect, one measures to the first individual and then assigns a perpendicular distance to the group center that is a randomly selected number between 0 and the perpendicular distance to the first individual (Buckland et al., 2010b). We follow this methodology for our Distance analyses, which we conducted using Conventional Distance Sampling (CDS) where we tested the hazard rate and half normal detection function models (cosine adjustment for each), truncated only the outliers because we already had small sample sizes, and used AIC to determine the best model (Buckland et al. 2001). We tested for significant differences by examining the overlap of 84% confidence intervals as this is equivalent to a significant difference at $\alpha = 0.05$ and therefore useful for programs like Distance that do not include significance tests (MacGregor-Fors and Payton, 2013).

The relationship between biological characteristics and edge presence. To examine the influence of biological characteristics (body weight, diet, group size, and

home range size) (Table 1) on primate presence in edges and interiors we used a binomial generalized linear model with a logit link and arcsine transformed the percent of fruit in the diet (*sensu* Boyle and Smith, 2010); we did not separately consider the percentage of seeds in the diet. We scored each transect 1/0 for the presence/absence of each primate species over all samples.

Alpha levels for all analyses were set at $P \leq 0.05$. All tests were conducted in SPSS version 19.0.0.1 and Distance version 6.0 (release 2).

RESULTS

Kruskal–Wallis tests on the average perpendicular distance to the trail (used to calculate density) did not significantly differ between the seven habitats (*Alouatta*: $\chi^2 = 5.144$, $df = 3$, $P = 0.16$; *Ateles*: $\chi^2 = 1.790$, $df = 2$, $P = 0.41$; *Chiropotes*: $\chi^2 = 4.082$, $df = 4$, $P = 0.40$; *Pithecia*: $\chi^2 = 5.114$, $df = 4$, $P = 0.28$; *Saguinus*: $\chi^2 = 8.835$, $df = 4$, $P = 0.12$; *Sapajus*: $\chi^2 = 1.847$, $df = 5$, $P = 0.87$). Mann–Whitney *U*-tests on perpendicular distances in mature vs. secondary forest revealed that only the data for *Alouatta* could not be combined (Table 2).

Our analysis of whether or not we could combine undisturbed primary forest transects (five) with selectively logged primary forest transects (two) to look for edge effects in each individual primate species found no interhabitat differences in average DBH ($N = 2274$,

$t = -0.122$, $P = 0.903$; undisturbed primary forest $N = 1627$, $\mu = 21.3$ cm, $SD = 12.5$ cm; selectively logged primary forest $N = 647$, $\mu = 21.4$ cm, $SD = 13.9$ cm) or stems/ha ($N = 7$; mean rank: primary = 4.40, logged = 3.00; $U = 3.000$; $Z = -0.775$; $P = 0.571$; undisturbed primary forest $N = 5$, $\mu = 795.4$, $SD = 72.5$; selectively logged primary forest $N = 2$, $\mu = 774.0$, $SD = 17.0$). However, there were interhabitat density differences for all species but *Ateles*, so our sample testing for edge effects in *Alouatta*, *Chiropotes*, *Pithecia*, *Saguinus*, and *Sapajus* is drawn from only the five undisturbed primary forest transects while data for *Ateles* also include the two logged primary forest transects.

We detected a large, but nonsignificant, difference in the number of large trees ($DBH \geq 60$ cm) in undisturbed primary forest edge (0–150 m) vs. interior habitats ($N = 10$, Edge: 6.7 ± 9.1 SD, Interior: 18.3 ± 9.4 SD, $Z = 1.803$, $P = 0.095$). A larger sample including both undisturbed primary forest and lightly selectively logged forest, which is relevant for our *Ateles* analyses (see above), shows significantly fewer large trees at the edge than in the interior ($N = 14$, Edge: 4.8 ± 8.1 SD, Interior: 18.0 ± 9.4 SD, $Z = 2.446$, $P = 0.017$).

Edge effects in population density (Whitesides Method) did not extend beyond 150 m (i.e., they were not evident in the 150–300 m edge class) for any primate species (Table 3). We found significant differences in population density (Whitesides Method) between the 0–150-m edge class and the forest interior for five of the six study species (Table 4). Data analyzed using the Distance Method followed the same pattern, save for a small change for *Pithecia*, but differences were not statistically significant due to the limitations of our data for this method, as discussed above (Table 4). (Note: because we did not test intervals shorter than 150 m, actual edge penetration distances for each species may be slightly greater or less than 150 m.) The full GEE models (including density (Whitesides Method), the number of large trees, and edge penetration depths of 0–150 m) showed that habitat remained significant for four species (*Alouatta*, *Chiropotes*, *Saguinus*, and *Sapajus*) while the number of large trees was significant for three (*Ateles*, *Chiropotes*, and *Sapajus*) (Table 5).

TABLE 2. Results of Mann–Whitney tests for interhabitat differences in perpendicular sighting distances

Species	Sample size		Mean perpendicular distance (m)		<i>P</i>
	Mature forest	Secondary forest	Mature forest (SD)	Secondary forest (SD)	
<i>Alouatta</i>	53	2	20.7 (12.1)	5.0 (2.8)	0.03
<i>Ateles</i>	22	0	23.3 (17.9)	n/a	n/a
<i>Chiropotes</i>	36	4	26.6 (23.7)	10.0 (10.2)	0.07
<i>Pithecia</i>	16	5	21.9 (15.9)	12.2 (7.9)	0.21
<i>Saguinus</i>	37	37	17.2 (11.9)	14.1 (10.0)	0.28
<i>Sapajus</i>	36	23	23.3 (15.5)	26.4 (25.4)	0.98

TABLE 3. Intraspecific density differences (Whitesides Method) over two edges zones and forest interior

Habitat	<i>Alouatta</i>	<i>Ateles</i>	<i>Chiropotes</i>	<i>Pithecia</i> *	<i>Saguinus</i>	<i>Sapajus</i>
0–150 m	11.1 ± 2.1^a	0.4 ± 0.2^b	$15.3 \pm 2.1^{c,d}$	n/a	10.5 ± 2.2^e	$18.6 \pm 2.0^{f,g}$
150–300 m	6.6 ± 1.5	1.1 ± 0.4	4.0 ± 1.0^c	n/a	4.8 ± 1.5^e	6.0 ± 1.0^f
Interior	6.6 ± 0.8^a	1.4 ± 0.2^b	3.2 ± 0.4^d	n/a	5.9 ± 0.8	6.5 ± 0.6^g

Estimated marginal mean \pm standard error (individuals/km²).

Letters (a-g) denote significant pairwise differences ($P \leq 0.05$).

*Not tested because there were no differences in the initial two-zone test.

TABLE 4. Intraspecific density differences (individuals/km²) by edge zone (0–150 m vs. forest interior)

Habitat	<i>Alouatta</i>	<i>Ateles</i>	<i>Chiropotes</i>	<i>Pithecia</i>	<i>Saguinus</i>	<i>Sapajus</i>	Method
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	
0–150 m	$11.1 (2.1)^a$	$0.4 (0.2)^b$	$15.3 (2.1)^c$	2.6 (0.8)	$10.5 (2.2)^d$	$18.6 (2.0)^e$	Whitesides
Interior	$6.6 (1.5)^a$	$1.1 (0.4)^b$	$4.0 (1.0)^c$	2.3 (0.3)	$4.8 (1.5)^d$	$6.0 (1.0)^e$	
0–150 m	13.4 (5.6)	0.7 (0.7)	15.7 (8.2)	2.3 (2.3)	15.4 (4.8)	15.2 (7.2)	Distance
Interior	9.1 (1.7)	2.0 (0.7)	5.0 (2.0)	3.2 (1.3)	7.5 (4.8)	8.0 (3.1)	

Data from the Whitesides Method are estimated marginal means.

Letters (a-e) denote significant pairwise differences ($P \leq 0.05$).

TABLE 5. Effect sizes (β) for the full model showing the influence of habitat (0–150 m vs. interior) and the number of large trees on primate density

Species	Intercept ^a	Habitat (Edge) ^a	Large Trees/ha ^a
<i>Alouatta</i>	1.757*	0.602*	0.006
<i>Ateles</i>	-1.583*	-0.022	0.092*
<i>Chiropotes</i>	-0.365	2.398*	0.074*
<i>Pithecia</i> ^b	n/a	n/a	n/a
<i>Saguinus</i>	1.527*	0.732*	0.012
<i>Sapajus</i>	1.386*	1.364*	0.023*

^a df = 1.

^b Not tested due to neutral edge response.

* $P \leq 0.05$.

At the forest edge (0–150 m) the overall model using biological characteristics to predict habitat use was not significant, though the percent of fruit in the diet was a significant predictor (as was the model with fruit in the diet as the only term (Table 6). In the forest interior neither the overall model nor any of the predictors was significant (Table 6).

DISCUSSION

Five of the six species in this study experienced significant edge-related changes in population density (as calculated using the Whitesides Method). These patterns were confirmed using the Distance Method, though the limitations of our data discussed earlier prevented the finding of significant differences using this methodology. Edge effects in primate density penetrated to ~150 m, the same distance over which the strongest edge effects in the plant community occur (Wandelli, 1991; Laurance, 1991; Camargo, 1993; Kapos et al., 1993; Laurance et al., 2000). This suggests that primates are responding directly or indirectly to edge-related floral changes. The prevalence of primate edge effects is also important because the mature forest edge sampled in this study now abuts 19–30-year-old secondary forests, illustrating that primates are impacted by habitat edges well beyond edge closure and the initial stages of matrix regeneration. Our data do not, however, permit the examination of edge effects in forests that border active agricultural lands, and it is entirely possible that primate edge effects in those habitats differ from those discussed here.

Edge effects in the densities of individual primate species were positive (*Alouatta*, *Chiropotes*, *Saguinus*, and *Sapajus*), negative (*Ateles*), and neutral (*Pithecia*). The positive response by *Alouatta* was explained by habitat type (edge vs. interior) with no significant influence of the number of large trees. Folivorous howler monkeys likely succeed in edges because they contain abundant pioneer tree species with weakly chemically defended foliage due to the increased mortality of large trees and higher treefall rates (Coley, 1980). Elevated light levels at the edge also bolster the production of poorly defended new leaves by mature forest species (Coley, 1980; Williams-Linera, 1990; Chen et al., 1992) and spur an increase in leaf protein concentrations that may make edge habitats attractive to arboreal folivores (Ganzhorn, 1995).

Although we predicted neutral edge responses, *Chiropotes*, *Saguinus*, and *Sapajus* had higher densities in edge habitats than in the interior. Traditionally *Chiropotes* is thought to be most abundant in undisturbed primary forest (Mittermeier, 1977; Ayers, 1989); however,

TABLE 6. Effect sizes (β) for the model examining the influence of biological characteristics on primate presence in edges

Habitat	Intercept ^a	% Fruit in the diet ^a	Weight ^a	Group size ^a	Home range ^a
0–150 m ^b	5.880*	-5.698*	-0.238	0.174	-0.005
0–150 m ^c	6.199*	-2.781*	—	—	—
Interior ^d	5.077	-2.111	-0.021	-0.111	<0.001

^a df = 1.

^b Overall model $\chi^2 = 7.883$, df = 4, $P = 0.096$.

^c Model testing only fruit: Overall model $\chi^2 = 5.058$, df = 1, $P = 0.025$.

^d Overall model $\chi^2 = 3.739$, df = 4, $P = 0.443$.

* $P \leq 0.05$

our results support other research at the BDFFP that shows that they utilize disturbed habitats (secondary forest, habitat fragments, and fragment edges) (Boyle et al., 2009; Lenz, 2013). In our model, habitat strongly predicted density while the number of large trees was much less important. We see several possibilities driving edge attractiveness for this species. First, the dense understory at the edge may appeal to *Chiropotes* because it facilitates their preference for feeding in the canopy but traveling in the understory (van Roosmalen et al., 1981; Walker, 1993). Second, *Chiropotes* specializes on the seeds of mature forest tree species and may frequent the edge because it is possible, though to the best of our knowledge unexamined, that the elevated light levels that spur foliage production and quality at the edge may also lead to increased seed production and/or quality. However, it is unlikely that *Chiropotes* utilizes the small, sugary, and nutrient poor fruits that often characterize the secondary tree species that invade edges (Grieser Johns 1997), something which might counteract potential increases in seed production by mature forest trees. The positive edge effect observed in *Chiropotes* could also be an artifact of their occasional associations with *Sapajus* at the study site (Lenz 2013), a species that spends a lot of time in habitat edges and the secondary forests that they border.

We hypothesized that *Saguinus* and *Sapajus* would show neutral edge effects because they utilize primary and secondary forest and would therefore view the edge as a transition zone between two habitats that they frequent. Instead, both species exhibited a positive edge response with higher densities in edge habitats. The number of large trees was also a weak predictor for *Sapajus* and nonsignificant for *Saguinus*. This pattern may be explained by diet as these species consume significant amounts of insects, which are known to be more abundant at the edge (Fowler et al., 1993; Malcolm, 1997). These are also the only primates whose highest densities were recorded in secondary forest at the study site, suggesting that the groups that heavily utilize secondary forest also make frequent use of mature forest edge habitats given their proximity to them. This is possible for two reasons: 1) we hypothesize that edges may offer vertebrate prey, plant foods, or sources of canopy water that are not readily available in the drier secondary growth, and 2) edges may contain preferred sleep sites for both species. Indeed, *Sapajus* often uses areas with large palms for both food and sleep sites and, while these areas are typically associated with riparian habitat at the BDFFP, large palms are uncommon in the BDFFP's secondary forests (Lenz, unpublished data;

Spirorello, 1991, 2001). While there are almost certainly *Saguinus* groups that sleep in secondary forest, in mature forest they frequently sleep in large trees with high canopies (Day and Elwood, 1999), suggesting that groups whose home ranges include mature and secondary forest may seek mature forest sleep sites in habitat edges.

The data support our prediction of a negative edge response by *Ateles*, confirming prior observations elsewhere (Mittermeier and van Roosmalen, 1981; Lehman, 2004). However, in the full model, habitat (edge vs. interior) was no longer significant while the number of large trees explained density patterns. Given that spider monkeys specialize on the fruit of large mature forest trees (van Roosmalen, 1985) it is probable that the decline in these trees in edge habitats (Laurance, 1991; Camargo, 1993; Kapos et al., 1993; Laurance et al., 2000; this study) leads to reductions in food availability for spider monkeys. *Ateles* also spends most of its time high in the canopy (25–30 m) (van Roosmalen and Klein, 1988; Lenz, 2013) and travels great distances each day due to its dependence on clumped fruit resources (Collins and Durbach, 2000). This pattern of range use may render many edge habitats unsuitable due to their numerous treefall gaps and decreased canopy connectivity that hinder locomotion (Wandelli, 1991; Kapos et al., 1993).

Pithecia was the only species to exhibit a neutral edge response. We predicted a positive response, assuming edge habitats would resemble preferred *Pithecia* habitats: areas with lianas, few large trees, and common small trees that permit locomotion and feeding in the lower and middle forest strata (Schwarzkopf and Rylands, 1989; Walker, 1996). The unexpected neutral edge response may be the result of interspecific competition with the other seed predator, *Chiropotes*, which displayed a positive edge response. Indeed, competition between the BDFFP's primate seed predators may be important as there is evidence of competition between their congeners, *C. albinasus* and *P. irrorata*, which occur at lower densities in sympatry than in allopatry (Ferrari et al., 1999). It is possible that we simply failed to detect the hypothesized positive edge effect due to small sample size. It may also be that habitat edges neither attract nor deter *Pithecia* and this species truly does not alter its behavior in response to habitat edges.

At the forest edge, we expected both the percentage of fruit in the diet and body size to explain primate presence, but only the former was relevant. The negative relationship between percent of fruit in the diet and primate presence suggests a reduction in fruit availability in edge habitats. This pattern is driven by the positive edge response in the three species that consume the least fruit (*Alouatta*, *Saguinus*, and *Sapajus*) and the negative response by the most frugivorous species (*Ateles*). We incorrectly predicted that forest structure at the edge (e.g., lower canopy heights and increased treefalls) would limit the presence of large primates. While the largest species (*Ateles*) avoided the edge, four of the remaining five species ranging from the smallest (*Saguinus*) to the second largest (*Alouatta*) exhibited positive edge responses. This indicates that decades-old habitat edges contain enough large trees to support heavier species but may contain an insufficient number of these trees to allow frequent edge use by species like *Ateles* that specialize on large trees for food and locomotor substrates (van Roosmalen, 1985; van Roosmalen and Klein, 1988; Lenz, 2013). As anticipated, there were no rela-

tionships between any biological characteristics and primate presence in the forest interior.

This study's primary limitations are that we lack detailed data on the diets of the primate community and that we were unable to sample edges that border active pastures. In terms of the latter, in these habitats one might expect negative edge effects to be more prevalent because: 1) the potential to move through edge habitats to utilize secondary forests, something which appears important at the BDFFP, does not exist, and 2) the floral edge effects to which primates appear to respond may be stronger due to drier conditions in the absence of secondary forest (Didham and Lawton, 1999). However, studies of edge use in habitats that border secondary forests remain important because knowledge of the use of these edges is necessary for projects that seek to expand/connect reserves through the management of secondary forests to create additional primate habitat and/or habitat corridors.

CONCLUSIONS

We detected edge effects to 150 m which, considering the rate of formation of Amazonian habitat edges of 50,000 km/yr (Broadbent et al., 2008), means that 750,000 ha of new edge habitats are created for primates each year. We have also shown that primates respond to habitat edges even following 19–30 years of matrix regeneration. That edges influence primates after such long periods demonstrates that anthropogenic edges have a potentially enormous impact on primates across the Amazon (e.g., combining the edge formation rate above with a 30-year window for primate edge effects yields 22.5 million ha of edge habitat). Our findings suggest that the impacts of the increasing prevalence of habitat edges will be most severe for the species that rely on large trees for food and/or locomotion. These species are also frequently large (e.g., *Ateles*) and therefore targeted by hunters (Peres, 1990). In landscapes where hunting is common, negative edge effects for these species will likely extend well beyond the 150-m ecological edge zone detected in this study to depths that approximate the distance into the forest that a hunter can travel from the surrounding anthropogenic matrix.

Positive and neutral edge responses allow land managers to consider the entirety of a mature forest to be viable primate habitat. Negative edge effects, particularly those that exist in spite of the presence of regenerating forests, reduce the amount of available habitat and signal a species (e.g., *Ateles*) with sensitive habitat requirements. However, even *Ateles*, which experienced negative edge effects and was never recorded in secondary forest during this study, still crossed both habitats on rare occasions to spend brief periods in habitat fragments (Boyle et al., 2013; Lenz, 2013). These findings are good news for conservationists because they show that even the most ecologically sensitive primates can disperse through habitats in which they do not thrive, thereby allowing the maintenance of gene flow and the recolonization of suitable forests.

Habitat edges may also influence parasite loads and predation pressure. Several studies have found that primate groups inhabiting small forest fragments (Gilbert, 1994) and edge habitats (Chapman et al., 2006) can have increased parasite infection rates, although this pattern does not always exist (Perea-Rodriguez et al., 2010). As one of the primary drivers of parasite species richness in primates is population density (Nunn et al.,

2003), it is possible that the four species in this study with positive edge effects in population density are negatively impacted by higher parasite loads.

Primate predation at the BDFFP has been observed both at the edge of a fragment (Gilbert, 2000) as well as in the forest interior (Lenz and dos Reis, 2011). Our encounters with potential primate predators and evidence of their presence during this study were distributed over all habitats, suggesting that there may not be an edge effect in predation pressure (Lenz, 2013). Studies of predation edge effects often examine avian nest predation, frequently finding no edge effect, or focus on temperate mesopredators (Cervinka, et al., 2011; Salek, et al., 2010). These findings may not extrapolate well to the large mammals and large raptors that are primate predators. Many primate predators have enormous home ranges [e.g., Harpy Eagle (*Harpia harpyja*): $\geq 4,300$ ha and jaguar (*Panthera onca*): 130–283 km² or greater in Amazonian Peru (Tobler et al., 2013)] that likely prohibit a focus on narrow edge habitats. However, while anthropogenic edges in and of themselves may not result in increased predation in edge habitats, the anthropogenic landscapes that border edge habitats are often hostile to large predators (e.g., Balme et al., 2010; Herremans-Tonnoeyr, 2000) and primates in edge habitats may therefore experience lower predation pressure where human presence in the matrix is significant.

The general pattern of primate success in, and recolonization of, the BDFFP's habitat fragments more or less mirrors the edge responses found in this study. *Alouatta*, *Saguinus*, *Pithecia*, *Sapajus*, and *Chiropotes*, in approximately that order, were the first to return to/remain in the fragments following their isolation (Boyle et al., 2013). These species also experienced positive or neutral edge effects. *Ateles*, the only species to experience negative edge effects, rarely uses habitat fragments (Boyle et al., 2013). Edge and fragmentation responses may therefore be driven by the same suite of behavioral and ecological traits, a logical supposition because habitat fragments are heavily impacted by edge effects (Laurance et al., 2011). As a result, where data are available for only edge or fragmentation responses, one might hypothesize similar primate responses to both phenomena.

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