Terrestrial mammal responses to edges in Amazonian forest patches: a study based on track stations

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Abstract

Examining edge effects is imperative to developing effective conservation and management strategies in fragmented landscapes as they are a key component of how landscape change influences habitat quality. Although medium- to large-bodied mammals are recognised as key components of tropical forests, their responses to forest edges remain poorly documented. Here, we describe how five species of medium- to large-bodied terrestrial neotropical mammals respond to forest-pasture edges along 17 forest patches (ranging in size from 5–4714 ha) and two continuous areas of Amazonian forest in Alta Floresta, Brazil. Tracks from two rodent (*Dasyprocta agouti* and *Agouti paca*) and three ungulate species (*Tayassu tajacu*, *Mazama gouazoubira* and *Tapirus terrestris*) were recorded over 4900 sand track station nights during a 4-month study period. When species occurrences were compared between patch size classes we found a significant interaction between patch size and distance from the nearest forest edge only for ungulates. We discuss the cost-effectiveness of monitoring protocols for large terrestrial mammals in tropical forests based on sand track stations, and how edge effects and patch size can modulate species abundance and distribution.

Keywords: edge effect; habitat fragmentation; herbivore; mammal surveys; neotropical forest.

Introduction

Brazil is experiencing the highest net loss of forest across the globe (estimated at 3.1 Mha/year: Food and Agriculture Organisation of the United Nations 2005) with most of this deforestation occurring in the Amazon basin (2.3 Mha in 2002, rising to >2.7 Mha in 2004: INPE 2005). However, these figures do not take into account the additional area altered by fragmentation and edge effects, which may be 150% or larger than the total area deforested (Skole and Tucker 1993). Ultimately, the myriad abiotic and biotic changes caused by edge creation and exposure to the surrounding matrix influence species persistence in fragmented habitats (Murcia 1995, Fahrig 2003).

Although the response of many vertebrate and invertebrate taxa to tropical forest edges has been investigated (birds: Restrepo and Gomez 1998, Lindenmayer et al. 2002; beetles: Didham et al. 1998, Ewers et al. 2007; reptiles: Schlaepfer and Gavin 2001; small mammals: Stevens and Husband 1998, Kristan et al. 2003), the response of large terrestrial mammals in the neotropics has yet to be described. Large terrestrial mammals are well recognised as a key component of tropical forest systems, largely through their effects on floristic structure and composition (Asquith et al. 1997, Terborgh et al. 2001, Fragoso et al. 2003, Pimentel and Tabarelli 2004, Stoner et al. 2007). Understanding how large mammals respond to forest edges is therefore important for conservation planning of increasingly fragmented neotropical forests.

The distance of edge influence is commonly used to quantify biotic responses to habitat edges (Ries et al. 2004, Harper et al. 2005). Previous studies have shown that average distances of edge influence generally extend <150 m from the forest edge (Laurance et al. 2002, Harper et al. 2005). This approach is amenable to relatively sedentary species or those that can be easily trapped or followed over relatively short distances, but large mammals do not generally fit these criteria. They are notoriously difficult to study even using time-consuming or capital-intensive techniques due to low population densities and secretive behaviour. This may help explain their conspicuous absence from the neotropical "edge effects" literature.

The difficulty in applying direct survey techniques, including line-transect or mark-recapture censuses to study cryptic or elusive terrestrial mammal species, has led to a number of indirect sampling methods, including track monitoring protocols (Wilson et al. 1996). Monitoring tracks has been used to derive indices of relative abundance, identify individuals and distinguish gender (Smallwood and Fitzhugh 1995, Stander et al. 1997, Jewell et al. 2001, Prada 2001, Crooks 2002, Pardini et al. 2003, Sharma et al. 2003). Here, we present a case study using this technique in a highly fragmented region of southern Amazonia to record the responses of medium- to large-bodied terrestrial mammals to forest edges, and discuss its cost-effectiveness and application in tropical field studies.

Methods

Study area

Fieldwork was conducted from April to August 2002 in a 1200-km² study area surrounding the town of Alta Flo-

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resta, State of Mato Grosso, Brazil (09°53′ S, 56°28′ W). The forest landscape in this Amazonian deforestation frontier (Landsat ETM scene 227/67) is characterised by a matrix of cattle pasture interspersed with forest patches of varying size, connectivity and degree of disturbance (see Peres and Michalski 2006 for further details on the study area).

Sampling design

Terrestrial mammal surveys were carried out in two areas of continuous primary forest and 17 primary forest patches of varying degree of disturbance (mean area±SD=760±1122 ha, range=5–4714 ha; Figure 1). We categorised all sampling sites into four size classes: small (<50 ha), medium (80–400 ha), and large (>900 ha) isolates and continuous forest (Table 1).
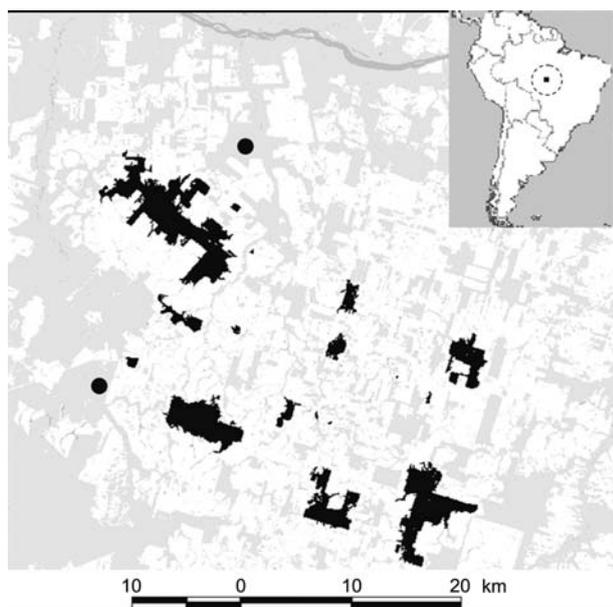
Figure 1 Alta Floresta study area, showing the location of 17 forest patches (solid black) and two continuous areas (solid black circles) surveyed.

Here, we focus on five mid-sized to large-bodied herbivore species: red-rumped agouti (*Dasyprocta agouti*), paca (*Agouti paca*), gray brocket deer (*Mazama gouazoubira*), collared peccary (*Tayassu tajacu*) and lowland tapir (*Tapirus terrestris*). These species are widely distributed in neotropical forests and illustrate variation in species track station visitation rate, despite high dietary overlap (Bodmer 1990, Asquith et al. 1997). They also encompass a wide spectrum of body mass and home range size, thereby enabling broad comparisons in terms of both sampling efficacy and responses to forest-pasture edges.

To evaluate the response of terrestrial mammals to forest edges, three 150-m transects were established in each forest site larger than 80 ha. Transects were separated by distances ranging from 150 to 500 m, using a random number generator to derive distance separator values and reduce spatial autocorrelation. The number of transects established in areas smaller than 80 ha depended on the distance separator value and on the size and shape of the patch. Transects were cut into each forest patch, following a compass bearing perpendicular to the edge adjacent to open cattle pastures.

Sand track stations were placed at distances of 0, 15, 45, 60, 75, 90, 105, 120, 135 and 150 m along each transect. Cattle ranchers often erected fencing at approximately 5 m from the forest border to separate pastures from an adjacent forest. Edges were therefore abrupt and regularly maintained in this region. As a result, the location of canopy trees in the original forest and the point of edge maintenance (border of regenerating undergrowth) were usually the same. When this was not the case, the initial track station (at 0 m) was placed to coincide with the most peripheral relict canopy trees.

To set up each track station, leaf litter, protruding roots, seedlings and stones were removed from a 1.5×1.5-m quadrat, and the area was firmed and levelled. Approximately 6 kg of sand was used per track station, arranged in a 0.75×0.75-m quadrat over the cleared area. A base of coarse sand (0.5–1 mm diameter, approximately 4 kg) was applied to level the substrate surface and then cov-

Table 1 Summary of the track station survey effort showing visitation rates of medium- to large-bodied herbivores monitored in each of four size classes of forest patch surrounding the Alta Floresta region, State of Mato Grosso, Brazil.

Patch category	Small	Medium	Large	Continuous
Patch size (n)	5–46 ha (7)	84–372 ha (5)	961–4714 ha (5)	Continuous (2)
Sampling effort				
Transects	13	15	15	6
Track station days	1300	1500	1500	600
Diversity (H)[a]	0.17 (0.09–0.25)	0.24 (0.10–0.41)	0.69 (0.50–0.88)	0.70 (0.56–0.82)
Visitation rate[b]				
Rodents	19.7 (12.9–26.6)	27.5 (17.9–39.5)	5.5 (3.3–8.1)	11.5 (8.3–15.0)
Dasyprocta agouti.	19.5 (12.4–26.7)	27.5 (17.4–38.8)	4.7 (2.6–7.2)	9.7 (7.0–12.8)
Agouti paca	0.4 (0–0.9)	0.3 (0.1–0.7)	0.9 (0.3–1.5)	1.7 (0.3–4.2)
Ungulates	0.5 (0.3–0.8)	1.0 (0.4–1.7)	1.9 (1.1–2.9)	2.3 (1.2–4.5)
Tapirus terrestris	0.2 (0.1–0.5)	0.5 (0.2–0.9)	0.4 (0.1–0.7)	2.1 (0.7–4.2)
Tayassu tajacu	0.1 (0–0.2)	0.2 (0–0.3)	0.9 (0.3–1.7)	0.3 (0–0.7)
Mazama gouazoubira	0.2 (0–0.4)	0.2 (0–0.3)	0.6 (0.2–1.1)	0.2 (0–0.5)
All species	20.5 (13.5–27.3)	29.1 (18.9–39.1)	7.4 (4.9–10.4)	14.0 (10.0–18.0)

[a]Mean diversity per 100 track station days, 95% confidence interval in parentheses.
[b]Mean number of records per 100 track station days, 95% confidence interval in parentheses.

ered with a layer of fine sand (0.1 mm diameter, 2 kg), which allowed tracks to be clearly distinguished.

All track stations were baited on a daily basis with a slice of fresh banana placed in the middle of the quadrat. When monitoring, any debris (e.g., leaves) on the track stations was first removed without disturbing the sand. The species identity of each track on each track station was then recorded with the assistance of local hunters who were familiar with tracks of all species, and then double-checked with the aid of field guides (Becker and Dalponte 1991, Emmons and Feer 1997). The surface of the track station was then smoothed and re-baited with a slice of banana.

As the clarity and shape of tracks deteriorate over time we monitored track stations daily, for a total of 10 days, interrupting bait application for 2 days after day 5 to reduce temporal autocorrelation. Stations were cleaned and bait was applied on the third rest day (day 8) and a further 5 days monitoring resumed the following day (day 9); providing a sampling effort of 100 track station days for each transect, and an overall sampling effort of 4900 track station days for all sites.

Dampness of the sand affected the size, shape and quality of track impressions. Therefore, it was necessary to control the moisture content of sand track stations to ensure clear track borders and consistent track identification. When there was no rain, we used a watering can to apply 1–2 l of water per track station every 2–3 days, depending on how quickly the sand dried out. Conversely, because tracks were often erased or distorted by heavy rainfall, monitoring days either following or during heavy rainfall were repeated to complete a total of 10 days.

Data analysis

A series of Mantel tests (Mantel 1967) were used to check for spatial autocorrelation in assemblage and individual species track station visitation rates (Bray-Curtis dissimilarity, untransformed data). All pairwise comparisons were examined based on 1000 iterations. To evaluate the influence of patch area on patterns of species accumulation and occurrence, we categorised areas into four size classes (Table 1). Species accumulation rates were obtained using curves derived from the average of 100 randomised iterations (Colwell 1997), providing a measure of the effort required to record the five focal herbivore species.

We used track station visitation rates to compare species occurrence and Shannon's diversity index H′ to compare the species composition between size classes. These measures were calculated for all transects in each size class. All means and 95% confidence intervals were calculated using bootstrap procedures with 10,000 iterations (Simon and Bruce 1991) (Table 1). Analysis of variance (ANOVA) was used to compare the variation in transect visitation rates and species composition between size classes. Visitation rates were square-root transformed to fit the assumption of normality. Post-hoc tests were conducted to identify distinct size classes.

To establish if changes in the occurrence of terrestrial herbivores were a function of distance and patch size, we analysed visitation rates for all species combined, and ungulates and rodents separately, using ANOVAs for mixed factorial designs. Patch size was included as a between-subject factor and distance to edge was included as a within-subject factor. Visitation rates for neighbouring pairs of track stations were summed to improve normality (0 and 15, 45 and 60, 75 and 90, 105 and 120, 135 and 150 m).

As no significant difference was found in species occurrence or composition, we also combined both the smallest (small and medium) and largest forest patch size classes (large and continuous) to form only two size classes, one comprising patches <400 ha, and the other >900 ha and continuous areas. The visitation rate data was then square-root transformed to reduce dimensionality and improve normality.

To remove the effect of patch area, we obtained the residuals from linear regression with $\log_{10}$-transformed patch area as a predictor of all species, rodents and ungulates visitation (square-root transformed). The ANOVA was repeated with residuals allowing us to evaluate responses to edge independently of patch area.

Species level trends in track station visitation in relation to distance from edges were analysed using a resampling approach. The proportion of records of each species was calculated per distance category for each size class. The slope of the trend across distance categories was then calculated as a measure of the strength and direction of response to edge. To determine if the calculated slope could occur by random chance alone, records were resampled without replacement between distance categories within each size class and the slope recalculated through 10,000 iterations (Manly 1997).

Results

Track station visitation

From April to September 2002, we accumulated 917 records of the five ubiquitous mammal species, amounting to an overall visitation rate for transects of 10 track stations of 18.1% (range: 13.8–23.1%). *D. agouti* was the most frequently recorded species in all patch size classes (mean visitation of 19.5%, 27.5%, 4.7%, 9.7%, classes small to continuous, respectively), but had the highest visitation rates in the two smallest size classes (small and medium) (Table 1). All other species were recorded at higher rates in the two largest classes (large and continuous) (Table 1).

Track stations were considered statistically independent as no significant association was found between either assemblage or individual species abundance dissimilarity and the linear distance separating track stations (Mantel test: assemblage r=-0.013, p=0.201; paca r=-0.009, p=0.346; agouti r=-0.013, p=0.067; brocket deer r=0.015, p=0.25; collared peccary r=0.003, p=0.429; lowland tapir r=0.009, p=0.335). We therefore retained individual track stations as the sampling unit for comparison of species accumulation rates between size classes.

Species accumulation curves showed two distinct groups, with continuous forest and large forest patches showing higher accumulation rates compared with those

of small and medium forest patches. Curves for large and continuous sites reached an asymptote, with all five species recorded at 501 and 710 track station days, respectively. Curves for small and medium classes also reached an asymptote, but more effort was required to record these five species (1450 and 1220 track station days, respectively).

Responses to edges

Forest patch size class significantly affected visitation rates of both rodents and ungulates (ANOVA, p=0.00015 and p=0.015, respectively; Table 2). However, the patterns differed between orders, with rodents showing a decrease in mean visitation, and ungulates showing an increase, with increasing patch size (Figure 2). Neither guild showed an overall significant effect of distance from edge on visitation rates (ANOVA, p=0.20 and p=0.22). However, the contrast of mean differences showed that ungulate visitation rates were higher at 150 m from the edge (mean=0.47) compared with the 0-m (mean=0.31) category ($F_{1,38}$=3.49, p=0.072).

Among ungulates, we found a significant interaction between distance to edge and patch size class for both the raw data (ANOVA, p=0.01, Table 2) and residuals (ANOVA, p=0.02, Table 2). Raw visitation rates at 150 m from the edge (mean=0.69) were significantly higher than at the edge (mean=0.18) in large forest patches, but were lower (mean at 150 m=0.05 compared with 0.21 at 0 m) in small patches (Figure 2, contrast of mean differences, $F_{1,38}$=8.02, p=0.007). Visitation rates in large patches at 150 m (mean=0.69) were significantly higher than those in patches <400 ha (mean=0.05), but no significant difference was found when visitation rates at 0 m, 60 m, 90 m and 120 m were compared between patches <400 ha and >900 ha.

The difference between rodent and ungulate responses to patch size class and distance from the edge is also demonstrated at the species level when the occurrence of *D. agouti* and *T. terrestris* were compared (Figure 3). Red-rumped agoutis showed no trend in response to distance from edge in small patches, whereas there was a significantly negative trend in the occurrence of lowland tapirs. Moreover, there was no trend in the occurrence of agoutis in large patches, but tapirs exhibited a significantly positive trend. Although it was not possible to evaluate how paca, gray brocket deer or collared peccary
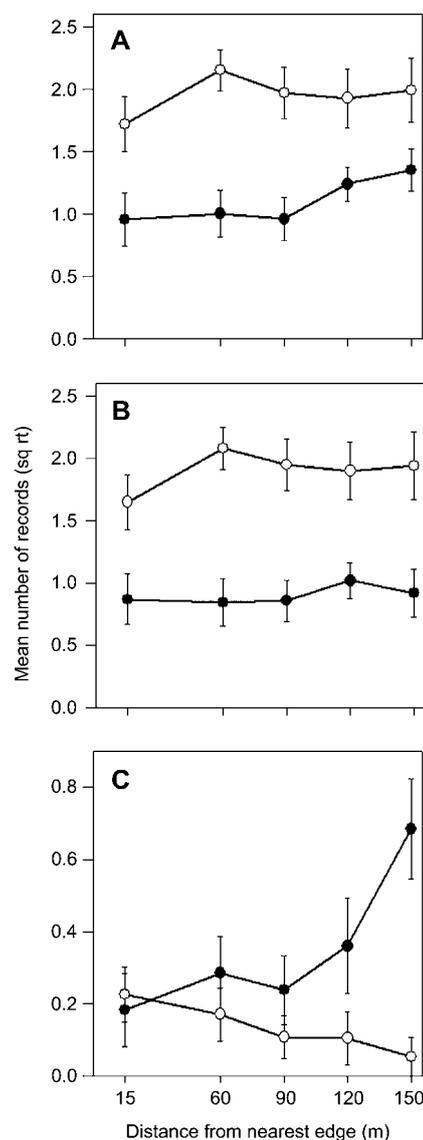
Figure 2 Occurrence of terrestrial herbivores (A=all species, B=rodents, C=ungulates) in relation to distance from nearest forest edge and patch size (open circles ≤372 ha, closed circles ≥961 ha). Points are mean visitations per 20 track station days (square-root transformed)±1 SE.

respond to edges in small patches due to small sample sizes, data are presented to allow discussion of the differences between rodents and ungulates.

Table 2 Results of three ANOVAs for mixed-factorial designs (1 between, and 1 within factor) on mean square-root transformed visitation rates×20 track station days of all herbivores, rodents and ungulates.

ANOVA	Class (df=1,38) F	Error: class (ss)	Distance from edge, DE (df=4,152) F_{H-F}	Class×DE (df=4,142) F_{H-F}	Error: DE×class (ss)
All	14.24***	19.86	2.19	1.74	79.49
All residuals	1.12	92.89	1.76	1.96	80.36
Rodents	17.72***	21.43	1.51	1.46	79.60
Rodents residuals	1.22	101.46	1.29	1.44	79.34
Ungulates	6.50*	2.51	1.44	3.39**	28.82
Ungulates residuals	0.65	12.30	1.37	3.52*	28.85

The F_{H-F} is the F-value based on the liberal Huynh-Feldt method.
*p<0.05; **p<0.01; ***p<0.001.
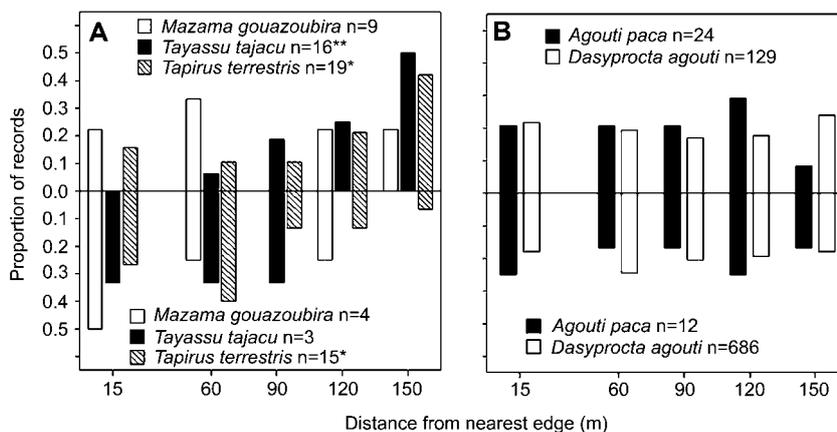
Figure 3 Species distribution in relation to distance from forest edge. Distribution of ungulate (A) and rodent (B) species along transects (n=49) intersecting forest patch edges. Values represent proportion of total visits by species at sand track stations arranged in five distance categories from the nearest forest edge-matrix border in large (>961 ha, above midpoint, n=7) and small (<372 ha, below midpoint, n=12) patches. *p<0.05, **p<0.01.

Discussion

The purpose of this study was to evaluate how a group of medium- to large-bodied terrestrial mammals respond to forest edges in a fragmented tropical forest landscape. We also present data on the efficacy of sand track stations for monitoring terrestrial mammals, which complements other large mammal studies based on track stations (Pardini et al. 2003). Our data demonstrate clear trends in relation to edge effects on large rodents and ungulates, as the first step towards a more detailed understanding of the responses of medium- to large-bodied neotropical terrestrial mammals to forest fragmentation.

Responses to forest edges

Terrestrial mammal visitation rates were higher in small forest patches (<400 ha). This pattern is explained by the high visitation rates of agoutis, the only species for which visitation rates were higher in small patches (<400 ha). This is potentially a cause for concern, as agoutis could disrupt forest regeneration as seed predators (Bierregaard et al. 2001). Any detrimental impact is likely to magnify and exacerbate the impacts of forest loss and fragmentation, which are known to cause tree species impoverishment in small forest areas (Gascon et al. 2000, Laurance et al. 2000).

Generalist species, such as *D. agouti*, were able to utilise forest areas of 5 ha or larger (Michalski and Peres 2007), as they are able to consume a wide variety of fruits and seeds (Henry 1999). In addition, predators, such as jaguar (*Panthera onca*), puma (*Puma concolor*) and ocelot (*Leopardus pardalis*), in the Alta Floresta region have been shown to have a less than 50% probability of occurring in forest patches smaller than 400 ha (Michalski and Peres 2005). Low predation rates may allow populations of these species to reach high densities compared with areas retaining a full complement of predators and could partly explain why more *D. agouti* records were obtained in small areas compared with large areas.

Cullen et al. (2001) found that agoutis were extirpated from Atlantic forest fragments of ~200 ha, whereas in Alta Floresta fragments of 80–400 ha had the highest relative abundances of this species. The most likely explanation for the observed differences between the two studies is that agoutis were hunted in the Atlantic forest sites studied by Cullen et al. (2001), whereas subsistence or recreational hunting in Alta Floresta does not significantly influence the abundance of agoutis or any of the other species in the present paper (Michalski and Peres 2007). Another possible explanation could be the presence of pre-equilibrium conditions due to relaxation time of the fragmentation process (Ferraz et al. 2003), because most of our forest fragments were younger than 20 years old compared to a much older fragmentation process in the Atlantic forest.

Our finding that rodent occurrence was not influenced by distance from edge is expected, as we would anticipate generalist species with small home ranges to be more resilient to biotic and abiotic changes at edges (Gotfryd and Hansell 1986, Nupp and Swihart 2000). *Dasyprocta* spp. and *Agouti* spp. have small home ranges, 3–8.5 ha and 0.7–3 ha, respectively (Smythe 1986, Beck-King et al. 1999, Silvius and Fragoso 2003, Jorge and Peres 2005), and when combined with a generalist frugivore-granivore diet may enable them to tolerate changes in forest habitat close to edges.

Both species are important seed predators and act as primary or secondary dispersers for a variety of tree species (Beck-King et al. 1999, Pimentel and Tabarelli 2004, Jorge and Peres 2005). They therefore likely affect seedling recruitment, plant spatial distribution and colonisation ability (Asquith et al. 1999, Terborgh et al. 2001). Understanding the impact of these species should be considered a priority for the formulation of effective management and regeneration programmes in the region.

In contrast to rodents, the distribution of ungulates based on visitation rates revealed a significant increase with patch size class. This result is consistent with findings from other sites (Glanz 1991, Wright et al. 1994) and the previously described higher persistence probability of

medium- to large-bodied vertebrates in the same region (Peres and Michalski 2006). We also found a significant interaction between distance to edge and patch size class for ungulates; with patterns of occurrence changing from a positive/neutral response to edges in small patches to a negative response in large patches.

Although edge effects are typically expected to work at a scale of around 150 m, Laurance (2000) suggested that this is expected to be a large underestimate for large-bodied mammals. We found that in fragments larger than 900 ha a significant increase in the relative abundance of ungulates was detected only at 150 m compared with 0 m, indicating that the degree of edge influences permeates beyond 150 m for this group in such areas. Data from five core forest transects (in three different large patches) with 10 track stations arranged from 350 to 500 m from the nearest edge also indicates that edge effects may permeate up to 365 m in such areas (D. Norris, unpublished data). Further research is required to determine if more subtle changes are detectable over the scale of several kilometres as predicted by Laurance (2000).

We expected a negative response to edges, as forest patches are a higher quality habitat than the pasture matrix for ungulates. Why then does the direction of ungulate responses to edges change with patch size class (Figures 2 and 3)? The difference in response could be purely an artefact of increasing patch size, which increases the core forest area that remains unaffected by changes at the edge. In other words, species that prefer primary/core forest conditions have more space to avoid transitional areas near edges in increasingly larger patches (Laurance and Yensen 1991). However, the observed difference was still apparent when the effect of patch size was removed suggesting that the change in response to edges between patch size class is not directly explained by increasing patch size.

Previous studies have shown that most of the unexplained variation in mammalian responses to edges came from positive/neutral observed responses when negative ones had been predicted; with "lack of information regarding resource distribution" proposed to explain such anomalies (Ries et al. 2004). However, our data suggest insight gained from such an analysis (considering edge effects in isolation) may be of limited value when applied to landscape scale assessments of large vertebrates. The finding that the direction of ungulate responses to edges changes with patch size suggests that broad scale fragmentation effects may be important to understand species responses to edges in our study region. We hypothesise that unpredicted changes in ungulate response in the region are a result of other fragmentation effects, i.e., spatial arrangement of patches within the landscape, connectivity and or proximity to continuous forest areas, and such factors will also have greater influences on the distribution and persistence of other mobile species.

Ungulates were able to use small forest fragments, which may only be visited intermittently for food or shelter, presumably because of their relatively large home ranges (Leeuwenberg and Leeuwenberg 1993, Fragoso et al. 2003, Keuroghlian et al. 2004) and ability to cross the matrix and overcome fencing erected to exclude cattle from the forest (Norris 2002). A positive/neutral response to edges in small areas could therefore be explained by a combination of two possibilities: (1) if patches are used intermittently then a positive/neutral response to edge may be expected as access to the matrix and other patches requires movements through the edge; and (2) if they are resident they must utilise all the available space to meet their metabolic requirements. Distance of edge influence is therefore unlikely to be an important determinant of ungulate species occurrence in areas smaller than 400 ha. However, the reduced abundance in small patches could be driven by edge effects (Ewers et al. 2007), as edge effects alone may ensure that small patches will be entirely low quality.

There is an increasing awareness of the dynamics of edge processes, but current models fail to incorporate such dynamism (Malcolm 2001, Ries et al. 2004). For example, these models examine response to habitat edges in isolation and do not take into account the spatial arrangement (e.g., proximity) of alternative habitat patches within the landscape. Our results for mobile species, such as tapir, suggest that such factors should be incorporated into models aimed at understanding ecological patterns and processes in fragmented landscapes and emphasise the importance of sampling the range of patch sizes relevant to the study species and landscape grain.

Use of track stations

Previous authors have suggested that indirect methods, such as track monitoring, are expensive to apply on a wide scale (Wilson et al. 1996). Our experience across a 1200-km^2 study landscape leads us to an alternative conclusion. In the Alta Floresta region, the financial investment required to sample each transect of 10 track stations was approximately US$1.20, equivalent to the local cost of sand and bananas – the only prerequisites to deploy this technique. When variable costs, such as labour and transport, were taken into account the investment increased to US$38.20 per transect, so there is still little financial constraint to increasing sampling effort by establishing a larger number of track stations.

The economy of using sand track stations is even more apparent when compared with the costs of commonly used alternative techniques (e.g., camera trapping). For example, the cost of sampling a transect at the same level using passive infrared camera traps would be approximately US$2255 based on the mean price of the five cheapest 22 photo-trap systems available via the internet. However, these costs could rise to at least US$3990 in the case of a more reliable, robust and easily programmable camera system, such as CamTrak phototraps ($399 each).

Although there seems to be little financial restriction in increasing sampling effort by establishing more track stations, the cost in terms of manpower can be a hindrance. In terms of personnel, this study required 6 person-days to establish three transects in an area, with three people spending 1 day cutting and marking transects and clearing track station areas, and 1 day carrying and distributing sand (approximately 200 kg/patch). Compared with

sand, camera trapping equipment is lightweight and fairly easy to handle, and as date and time are recorded, monitoring on a daily basis is not critical. Once established they need only be checked occasionally to change film and batteries (4 C-cells batteries in several phototrap systems can often last 45 days). Photo-trapping is therefore a far less labour-intensive and time-efficient monitoring technique (Foresman and Pearson 1998).

The demands for scientifically rigorous monitoring programmes are such that no single technique can be used to address all issues. Even with the uncertainties inherent in track identification we believe that the use of sand track stations has not been used to its full potential in replicable, comparative studies of species occupancy and habitat use. Sand track stations provide a cheap, easily repeatable method to obtain a large amount of data, over a large area, in a short space of time (Pardini et al. 2003). The accuracy of the data could then be improved by the use of camera traps on a smaller scale. By calibrating both of these indirect techniques with direct population estimates from line-transect census it may be possible to calibrate indices of relative abundance (Groves et al. 2002). Coarse scale track station data could thus help validate regional scale assessments.

Conclusion

We found no evidence to suggest a direct response to edges independent of forest patch area or patch size class by the species groups investigated. This suggests that these taxa are neither "forest interior" nor edge sensitive species, but either a) depend on forest habitat but are not sensitive to edges, or b) "edge species" that tolerate and may even thrive along forest edge conditions. Further, the response of mobile ungulate species are consistent with the 'synergistic' edge effect model presented by Ewers et al. (2007), but also suggests a change of emphasis from small- to medium- and large-bodied mammals is needed to advance understanding of forest fragmentation patterns and processes.

Although the role of mammals in tropical forests is relatively well documented (Terborgh et al. 2001, Stoner et al. 2007), most of the existing mammal studies in the fragmentation ecology literature are based on small mammals, e.g., rodents and marsupials accounted for 80% of mammal studies analysed by Reis et al. (2004). Moreover, the number of fragments studied and their range in size is often small (Fahrig 2003) and/or based on isolated islands (Terborgh et al. 2001), which means results are not necessarily applicable to fragmented landscapes in agricultural frontiers. Developing and applying cost- and time effective sampling techniques for highly mobile species, such as large mammals, is therefore vital to provide the empirical data upon which to build models that can predict both regional and landscape scale impacts of forest loss and fragmentation.

Acknowledgements

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