

HABITAT FRAGMENTATION AND EFFECTS OF HERBIVORE (HOWLER MONKEY) ABUNDANCES ON BIRD SPECIES RICHNESS

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Abstract. Habitat fragmentation can alter herbivore abundances, potentially causing changes in the plant community that can propagate through the food web and eventually influence other important taxonomic groups such as birds. Here we test the relationship between the density of red howler monkeys (*Alouatta seniculus*) and bird species richness on a large set of recently isolated land-bridge islands in Lago Guri, Venezuela ($n = 29$ islands). Several of these islands host relict populations of howler monkeys at densities up to more than 30 times greater than those on the mainland. These “hyperabundant” herbivores previously have been shown to have a strong positive influence on aboveground plant productivity. We predicted that this should lead to a positive, indirect effect of howler monkey density on bird species richness. After accounting for passive sampling (the tendency for species richness to be positively associated with island area, regardless of differences in habitat quality) we found a significant positive correlation between howler monkey density and bird species richness. A path analysis incorporating data on tree growth rates from a subset of islands ($n = 9$) supported the hypothesis that the effect of howler monkeys on the resident bird communities is indirect and is mediated through changes in plant productivity and habitat quality. These results highlight the potential for disparate taxonomic groups to be related through indirect interactions and trophic cascades.

Key words: *Alouatta seniculus*; bird species richness; faunal relaxation; grazing optimization; habitat fragmentation; herbivory; indirect effects; Lago Guri, Venezuela; passive sampling; red howler monkey; species–area relationship; tropical dry forest.

INTRODUCTION

Tropical forests are becoming increasingly fragmented due to high rates of deforestation and land conversion (Skole and Tucker 1993, Laurance and Bierregaard 1997, Wade et al. 2003). Most studies investigating the consequences of fragmentation have focused primarily on the direct impacts of area reduction on plant and animal communities and have not addressed the potential for subsequent indirect effects caused by ecological imbalances and altered trophic interactions. Here we report on a study linking changes in the bird communities inhabiting small tropical dry forest fragments with changes in the mammalian herbivore communities due to indirect effects and changes in plant productivity.

Studies of remnant forest fragments have found that the densities of mammalian herbivores can change significantly following habitat isolation (Saunders et al. 1991, Terborgh et al. 1997b, Cosson et al. 1999, Arnold and Asquith 2002, Dalecky et al. 2002, Estrada et al. 2002, Lambert et al. 2003). Changes in herbivore abun-

dances have been attributed variously to differences in predation pressure (Lambert et al. 2003) including hunting (Peres 2001), parasite loads, and/or resource availability (Milton 1982).

Whatever the cause(s), changes in herbivore abundances, in turn, may have important impacts on plant communities. Herbivores can influence the growth and survival of adult plants through the consumption of photosynthetic tissue (Coley 1982, de Mazencourt and Loreau 2000). Herbivores can also alter plant fecundity and reproduction either directly by consuming plant reproductive organs (flowers, fruits, seeds) or indirectly by inducing plants to shift the allocation of resources toward leaf defense and away from reproduction (Ruess and McNaughton 1984). In addition, terrestrial herbivores can have dramatic impacts on seedling and sapling communities, often reducing rates of recruitment and regeneration (Alverson et al. 1988, Dirzo and Miranda 1991, McShea et al. 1997). Finally, herbivores may affect rates of nutrient cycling through their consumption and defecation of plant nutrients (McNaughton 1976). Given the importance of herbivores in regulating plant communities, there is a strong potential for the altered mammalian communities persisting in forest fragments to have subsequent indirect effects on other taxonomic groups.

We investigated the effects of altered mammal communities in tropical forest fragments through a series

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of studies on several recently isolated land-bridge islands located in Lago Guri, Venezuela. Some of these islands support relict populations of herbivorous red howler monkeys (*Alouatta seniculus*) at densities that can exceed 8 individuals/ha (~20–40 times greater than those observed on the nearby mainland; Terborgh et al. 1997b). In a recent study, we found that the increased howler monkey density has resulted in increased tree growth rates, potentially due to accelerated nutrient cycling (Feeley and Terborgh 2005). Here we test the hypothesis that the increased productivity propagates through the food web to affect other members of the faunal community. Specifically, we test the relationship between howler monkeys and the species richness of resident forest-interior birds nesting on a large sample of islands in Lago Guri. For a subsample of islands, we analyze the relationship between tree growth rates and bird species richness and use path analysis to determine the magnitude of the indirect effect of howler monkeys on avian species richness as mediated through plant productivity.

METHODS

Lago Guri is a man-made hydroelectric reservoir that inundates ~4300 km² near the confluence of the Caroni and Orinoco Rivers in east-central Venezuela (Appendix A). The impoundment contains a large number of forested islands that range in area from <0.1 ha to >700 ha. Islands are isolated from the mainland by as much as 12 km (Morales and Gorzula 1986).

The numbers of resident forest-interior bird species nesting on 29 islands were estimated in 2000. Study islands were located in the west-central portion of the lake (Appendix A) and ranged in area from 0.2 to 21.4 ha (small [<2.5 ha] and medium [>2.5 , <25 ha] islands in the terminology of Terborgh et al. 1997a, b, 2001; see Appendix B). We elected not to include larger islands or the mainland because they could not be censused in their entirety, potentially introducing additional sources of error. Moreover, large islands and the mainland contain some faunal groups (large predators of vertebrates) and microhabitat types (e.g., palm patches, stream drainages) not present on either medium or small islands; thus the factors influencing resident avian communities may not be fully comparable. The mainland has also experienced a different disturbance regime than the islands (the mainland was high-graded for prime timber species during dam construction and has suffered repeated ground fires since inundation, presumably set by poachers), resulting in significant differences in both the structure and composition of the mainland forest relative to the islands. The final number of islands censused was based largely on logistical constraints.

The habitat of all study islands was semideciduous tropical dry forest (Huber 1986, Terborgh et al. 1997a), with a canopy height ranging from ~15 to 20 m and occasional emergents reaching 25 m. The mean annual

temperature recorded at the dam is 27.5°C, and annual rainfall is ~1000–1200 mm, with most precipitation occurring between the months of May and October (Alvarez et al. 1986).

Elsewhere, we have presented detailed descriptions of the methods used to census birds at Lago Guri (Terborgh et al. 1997a, b, Feeley 2003); only a brief overview is given here. We conducted a minimum of five spot-map censuses of each island during the first half of the rainy season (May through August), which coincides with the avian breeding season at Lago Guri. All censuses were conducted during hours of peak vocal activity (between 5:30 and 8:00 hours, local time). The order in which islands were censused, the direction in which the trails were walked, and the identity of the observer were all alternated in order to minimize potential bias. Censuses were not conducted during inclement weather (rain or strong winds).

Following the protocol of Terborgh et al. (1997a, b), all vocalizations and sightings of birds were identified and mapped. Males or pairs observed in less than two-thirds of the census visits to an island were classified as visitors and were excluded from the analyses. Lago Guri islands are surrounded by the snags of trees killed by inundation. These snags form a distinct matrix from the islands and are used by a number of bird species (e.g., some falcons, woodpeckers, flycatchers, martins, swallows) for nesting, foraging, and roosting. Such “edge” species are not dependent on the forest interior and thus were excluded from the analyses. In addition, we excluded species that we have observed to use large territories incorporating multiple islands (e.g., raptors, macaws, parrots, and large pigeons).

To analyze the potential effects of herbivores on the bird communities, it was necessary to first account for differences in species richness caused by the “passive sampling effect.” This term refers to the general tendency for large islands to host more species than small islands due simply to their greater area, irrespective of differences in habitat quality. Based on passive sampling alone, the number of nesting pairs on an island (I_i) is predicted to be directly proportional to relative area such that:

$$I_i = I_{\text{tot}} (A_i/A_{\text{tot}}) \quad (1)$$

where I_{tot} is the total number of pairs recorded for all islands; A_i is the area of island i ; and A_{tot} is the total area of all islands combined (Coleman et al. 1982). Using this equation, we calculated the expected number of pairs for each of the study islands. The predicted species richness (S_{pred}) of each island was then determined by sampling I pairs at random from the pooled list of all pairs from all 29 islands and counting the corresponding number of species. We iterated this process 10 000 times and calculated the median species richness predicted for each island. We then calculated the number of missing/extra species (B , residual bird species richness) for each of the islands as the differ-

ence between the observed and actual number of species, such that

$$B_i = S_{\text{obs},i} - S_{\text{pred},i} \quad (2)$$

where $S_{\text{obs},i}$ is the number of resident species observed on island i , and $S_{\text{pred},i}$ is the number of species predicted for the island based on passive sampling (Appendix B).

After accounting for passive sampling effects, we determined the relationship between B and howler monkey density. Estimates of howler monkey densities were based on mammal censuses conducted for all study islands in 1993, 1997, and 2000. Additional information on census methods is provided in Terborgh et al. (1997b, 2001).

The annual woody increment (AWI) is the change in basal area per hectare, an indicator of aboveground productivity in forested ecosystems (Sala and Austin 2000). AWI had previously been determined for nine of the study islands, originally selected to be representative of conditions on Guri islands, yet small enough to facilitate sampling. AWI was calculated by measuring the circumferences (in millimeters) of all living stems >10 cm diameter at breast height (dbh) in 2001 and 2002 and by calculating the total change in basal area per hectare (Appendix B; Feeley and Terborgh 2005). Although AWI was not calculated during the same year as bird species richness (2001–2002 vs. 2000), we believe that it is indicative of consistent differences in relative aboveground productivity between islands, especially because densities of howler monkeys, which have been shown to drive differences in tree growth rates at Lago Guri (Feeley and Terborgh 2005), have remained stable over the past several years.

In order to test if the relationship between howler monkeys and birds is mediated through changes in plant productivity, we used linear least square regression to analyze the relationship between AWI and B , and path analysis to determine the indirect effect of howler monkey density. Path coefficients (standardized regression coefficients) were calculated for the relationships between the density of howler monkeys and AWI ($P_{\text{H,AWI}}$) and between AWI and B ($P_{\text{AWI,B}}$). We calculated the path coefficient for the indirect relationship between howler monkey density and B ($P_{\text{H,B}}$) as the product of the two direct paths such that $P_{\text{H,B}} = P_{\text{H,AWI}}P_{\text{AWI,B}}$ (Sokal and Rohlf 1995).

RESULTS

The censuses yielded a total of 341 resident breeding pairs of 31 forest-interior bird species (Appendix C; Feeley 2003). Passive sampling alone accounted for 34% of the observed variation in species richness. Residual bird species richness (B) was 0.28 ± 5.51 species (mean \pm SD) and had a significant negative correlation with island area such that small islands were more diverse than predicted by passive sampling ($R = -0.58$, $P < 0.005$; Fig. 1a).

After accounting for passive sampling, there was a significant positive correlation between bird species richness (B) and the density of howler monkeys ($R = 0.59$, $P < 0.001$; Fig. 1b).

Tree growth rates were estimated from measurements of more than 1500 trees on nine small islands. Islands included in this subsample averaged 0.5 ± 0.3 ha and supported 0–8.6 howler monkeys/ha (Appendix B). Annual woody increment (AWI) averaged $0.16 \text{ m}^2/\text{ha}$ and increased significantly as a function of howler monkey density ($r^2 = 0.82$, $P < 0.001$). On average, AWI was over six times greater on islands with howler monkeys than on islands lacking monkeys (Appendix B; Feeley and Terborgh 2005). After accounting for differences in howler monkey density, there was no relationship between AWI and island area.

AWI had a significant positive effect on residual bird species richness ($B = 0.2 + 20.1 \text{ AWI}$; $r^2 = 0.48$, $P < 0.05$). Two islands, Colon and Facil, qualified as outliers based on Cook's distances and externally studentized residuals (Sokal and Rohlf 1995). If these two islands are excluded from the analysis, the relationship between AWI and B improves significantly ($B = 1.3 + 20.9 \text{ AWI}$; $r^2 = 0.94$, $P < 0.0005$; Fig. 2). The effect of AWI on bird species richness remains significant if raw species counts are used in place of B ($S_{\text{obs}} = 1.2 + 23.8 \text{ AWI}$; $r^2 = 0.51$, $P < 0.05$).

According to path analysis, the relationships between the density of howler monkeys and AWI ($P_{\text{H,AWI}}$) and between AWI and B ($P_{\text{AWI,B}}$) are 0.63 and 0.51, respectively. The indirect effect of howler monkey density on B ($P_{\text{H,B}}$) is 0.32 ($P < 0.005$). If the two potential outlier islands are excluded, $P_{\text{H,B}} = 0.37$ ($P < 0.005$). These results are consistent with the hypothesis that the positive relationship between howler monkey density and bird species richness is due to indirect effects mediated via accelerated plant productivity.

DISCUSSION

Numerous studies have found that the diversity of birds residing in fragments tends to decrease with area (Karr 1990, Stouffer and Bierregaard 1995, Brooks et al. 1999, Thiollay 2002, Ferraz et al. 2003). At least part of this area effect could be due to passive sampling, and may not reflect any true differences in habitat quality (Coleman et al. 1982). After taking the effects of passive sampling into account, we determined that the number of species nesting on islands in Lago Guri actually decreases with island area, but increases in relation to the density of howler monkeys.

Several small islands in Lago Guri support howler monkeys at densities many times greater than those found in natural systems. The increased abundance of generalist herbivores in forest fragments is not restricted to howler monkeys; many of the same islands included in this study also support hyperabundant populations of common iguanas (*Iguana iguana*) and leaf-cutter ants (*Atta* spp. and *Acromyrmex* sp.) (Terborgh

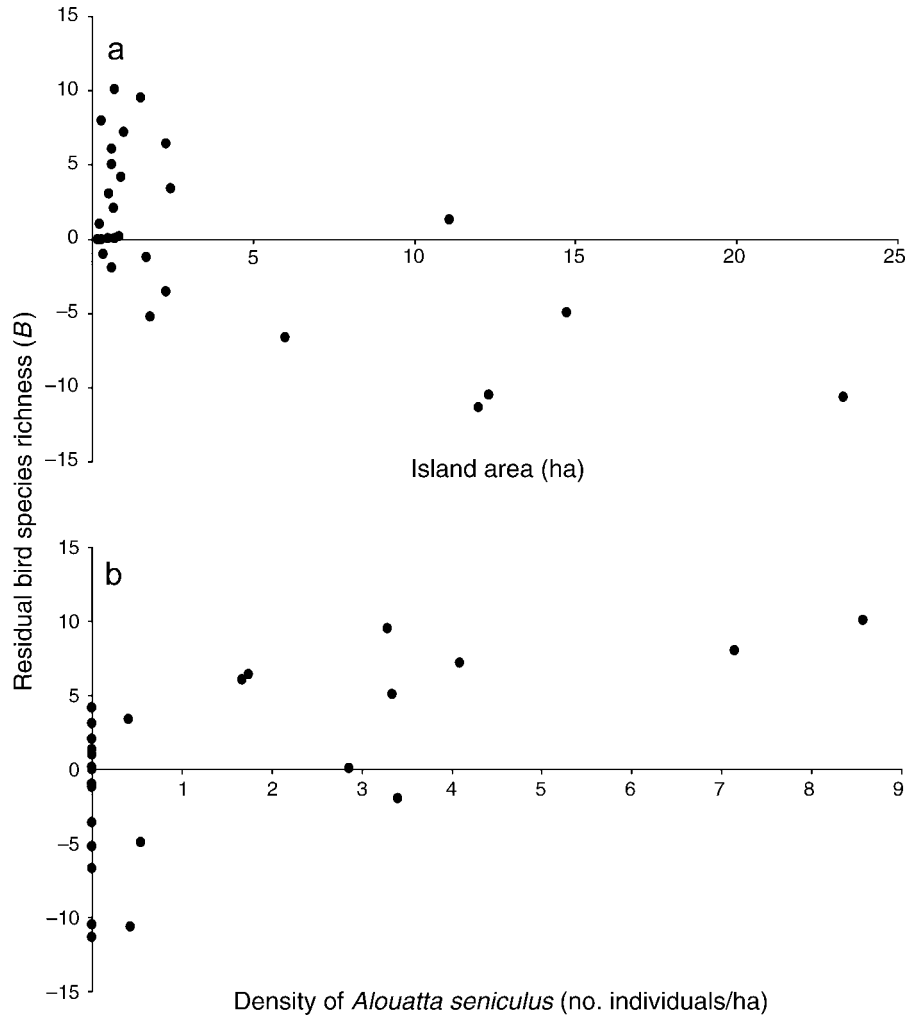


FIG. 1. The residual bird species richness on islands (a) decreases with island area ($R = -0.58, P < 0.005$) but (b) increases in relation to howler monkey density ($R = 0.59, P < 0.001$).

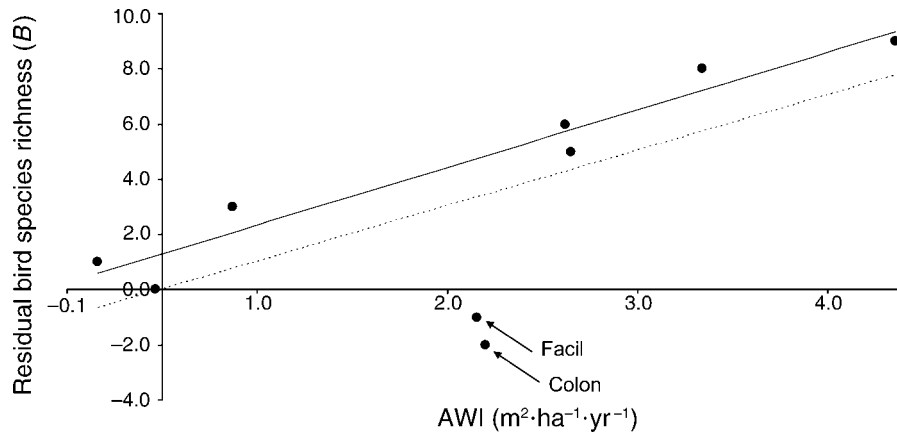


FIG. 2. The residual bird species richness (B) increases significantly with the annual woody increment (AWI). If all of the islands where AWI was measured ($n = 9$ islands) are included, the relationship is described by the linear function $B = 0.2 + 20.1(AWI)$ (solid line, $r^2 = 0.48, P < 0.05$). If Facil and Colon Islands are excluded as outliers, the relationship is significantly improved (dotted line, $B = 1.3 + 20.9(AWI); r^2 = 0.94, P < 0.0005$).

et al. 1997b, Rao 2000), nor is it unique to Lago Guri. In fact, the persistence of dense populations of howler monkeys and other generalist herbivores in small habitat fragments is widespread throughout much of the Neotropics, having been reported from Panama, Brazil, French Guiana, and Mexico (Milton 1982, Lovejoy et al. 1984, Schwarzkopf and Rylands 1989, Cosson et al. 1999, Estrada et al. 1999, Estrada et al. 2002).

Although the exact mechanisms allowing howler monkeys and other generalist herbivores to attain and maintain high densities in habitat fragments remain unresolved, increased herbivory pressure potentially can have important community-level consequences (Rao et al. 2001, Terborgh et al. 2001). Increased plant growth and aboveground productivity due to high levels of herbivory has been observed in many tropical and temperate ecosystems (McNaughton 1976, Coppock et al. 1983, Olofsson et al. 2001, Frank et al. 2002), including Lago Guri (Feeley and Terborgh 2005). This phenomenon, which is analogous to "grazing optimization" (McNaughton 1979), may be caused by an acceleration of the rate at which nutrients are recycled and made available for plant uptake due to the increased percentage of nutrients transferred through feces as opposed to leaf litter, throughfall, or other pathways (Feeley 2005, Feeley and Terborgh 2005).

Change in primary productivity can potentially propagate throughout the food web and have important effects on other organisms (Abrams 1993, Folkard and Smith 1995, Siemann 1998). Therefore, we predicted that the increase in tree growth rates caused by dense populations of howler monkeys should positively affect the number of bird species inhabiting the islands of Lago Guri, and should help to explain the observed correlation between howler monkey density and B . Consistent with this hypothesis, we found a significant positive effect of tree growth rates (AWI) on bird species richness (both B and S_{obs}) and a positive indirect effect of howler monkey density on bird species richness. Only a very small percentage of the Lago Guri bird community is directly dependent on plant productivity (i.e., frugivores, granivores, or nectivores). Rather, almost 80% of the bird species are either insectivores (45.2%) or omnivores (34.5%) (Appendix C) and therefore the relationship between plant productivity and bird species richness is hypothesized to be indirect and mediated primarily through insect abundances.

The relationship between AWI and bird species richness (and, consequently, the indirect relationship between howler monkey density and B) is significantly improved if two islands, Facil and Colon, are considered as outliers and excluded from the analysis. Although we do not know for certain why neither of these islands supported any birds in 2000, despite their relatively high AWI, it is interesting to note that Colon and Facil Islands are situated very close (<300 m) to one another (Appendix A). It is possible that some

edaphic or ecological condition (such as predator abundances) not considered in the current analyses extends between both islands and decreases the number of resident birds that the islands can support. In 1993 and 1995, Terborgh et al. (1997a) censused 10 pairs of eight bird species nesting on Colon Island; thus the complete absence of birds from this island in 2000 is a relatively recent phenomenon and may be only temporary (Facil Island was not formally censused prior to 2000).

The results of this study are consistent with our hypotheses; however, we were only able to analyze the indirect path between howler monkeys and birds for a small subset of islands for which data on AWI were available. All of these islands were "small" and thus it is possible that the relationship between howler monkeys and the bird communities is mediated through other, as of yet unidentified, pathways on larger islands. Alternatively, the relationship between howler monkeys and birds may not be causal, but due simply to similar habitat preferences. Although this hypothesis is difficult to address in the absence of large-scale experimental manipulations, we have presented evidence elsewhere (Feeley and Terborgh 2005) indicating that the distribution of howler monkeys is stable and appears to have been determined primarily by island isolation rather than by any initial differences in habitat quality or other environmental factors. For example, howler monkeys are missing from islands that can become temporarily connected with larger land masses during severe droughts. Birds, on the other hand, are much more mobile and are believed to be distributed primarily on the basis of habitat quality, as supported by the fact that there is no significant relationship between B and island isolation after accounting for differences in either howler monkey density ($P = 0.12$) or AWI ($P = 0.63$) (Appendix B).

CONCLUSION

Worldwide, humans are having dramatic impacts on the diversity and abundance of herbivores both directly through activities such as hunting, harvesting, and introductions, and indirectly through land conversion and habitat fragmentation. These changes potentially can have important impacts not only for plant communities, but also for other groups of animals through indirect trophic interactions (McShea and Rappole 2000). As the results of this study indicate, these indirect effects may play important roles in determining the diversity of faunal communities in forest fragments. We suggest that future research on fragmented habitats be designed to examine the indirect, as well as direct, effects of area reduction and isolation.

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APPENDIX A

A map of northeastern South America with the location of Lago Guri and study islands indicated (*Ecological Archives* E087-005-A1).

APPENDIX B

A table listing the characteristics of the study islands (*Ecological Archives* E087-005-A2).

APPENDIX C

A table listing the characteristics of bird species recorded as residing on the Lago Guri islands used in this study (*Ecological Archives* E087-005-A3).