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Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system

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ABSTRACT

Habitat fragmentation causes drastic changes in the biota and it is crucial to understand these modifications to mitigate its consequences. While studies on Neotropical bats have mainly targeted phyllostomid bats, impacts of fragmentation on the equally important aerial insectivores remain largely unexplored. We studied species richness, composition, count abundance and feeding activity of aerial insectivorous bats in a system of land-bridge islands in Panama with acoustic sampling. We predicted negative effects of fragmentation on forest species while bats foraging in open space should remain essentially unaffected. Rarefaction analyses indicated higher species richness for islands than mainland sites. For forest species, multivariate analyses suggested compositional differences between sites due to effects of isolation, area and vegetation structure. Contrary to our expectations, count abundance of forest species was similar across site categories. Feeding activity, however, was curtailed on far islands compared to near islands. As expected, bats hunting in open space did not reveal negative responses to fragmentation. Interestingly, they even displayed higher abundance counts on far and small islands. On the species level, two forest bats responded negatively to size reduction or site isolation, respectively, while a forest bat and a bat hunting in open space were more abundant on islands, irrespectively of island isolation or size. Our findings suggest that small forest remnants are of considerable conservation value as many aerial insectivores intensively use them. Hence high conservation priority should be given to retain or re-establish a high degree of forest integrity and low levels of isolation.

1. Introduction

It is now widely accepted that the pervasive biodiversity loss in tropical environments is powered by the conversion of forests into agricultural and grazing landscapes (Laurance and Peres, 2006). This produces a mosaic of isolated remnants, large and small, that harbors a partial selection of the original diversity, where species abundance, richness, and evenness have changed dramatically across taxonomic groups (Laurance et al., 2002; Ewers and Didham, 2006). Following such modifications, ecological interactions such as seed dispersal, pollination and insect predation are transformed, and terminated in the worst case scenario (Restrepo et al., 1999; Laurance et al., 2002).

Changes in assemblage structure in forest fragments are mediated by, among others, the type of matrix surrounding the remnants and by species' perceptions of the matrix (Kupfer et al., 2006). Matrices with low permeability reduce population connectivity among remnants and accentuate the effects of isolation regardless of the real inter-patch distance (Ricketts, 2001). However, tolerance of the matrix and dispersal ability will set the degree of inter-patch movement and therefore determine the species' sensitivity to fragmentation (Ewers and Didham, 2006; Meyer and Kalko, 2008).

Resource availability within fragments and the matrix also shape changes in assemblage structure. For example Gascon et al. (1999) have shown that birds, small mammals and frogs that avoid the matrix tend to decline in fragments while those that can use the matrix often remain stable or even increase in abundance. Finally, the level of contrast in vegetation between fragment and matrix, in addition to remnant size, produces edge effects that modify niche characteristics and ultimately affect animal assemblages (Watson, 2002). As an example, tropical birds and small terrestrial mammals show reduced richness, abundance and probability of

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occurrence in response to forest edges (Beier et al., 2002; Laurance et al., 2002; Lambert et al., 2003).

Bats are well-suited to examine fragmentation effects because they are highly mobile, and ecological diverse with a variety of feeding and roosting habits (Fenton et al., 1992; Gorresen and Willig, 2004; Meyer et al., 2008). While Neotropical bat assemblages are dominated by members of the endemic family Phyllostomidae (New World leaf-nosed bats), the other eight families found in the Americas are also species-rich. Almost half (46%) of the species of the entire bat assemblage known to occur on Barro Colorado Island, Panama, are non-phyllostomid bats (Kalko et al., 2008). Despite their species richness and their important role as control agents of insects (Cleveland et al., 2006) information about aerial insectivores in lowland rainforests is still scarce (Jung et al., 2007).

The ensemble of aerial insectivorous bats consists of species that rely on echolocation as their main sensory input to navigate, orient and forage, thereby capturing insects on the wing. They hunt either inside or above the forest canopy. These sensory capacities, in addition to morphology and foraging habits, allow the separation of aerial insectivorous bats into three functional groups: (1) bats that forage in highly-cluttered space, (2) background-cluttered space and (3) uncluttered space (sensu Schnitzler and Kalko, 2001). Bats hunting for insects in highly-cluttered space forage within vegetation and use special auditory adaptations (i.e., Doppler shift compensation) for prey detection whereas species foraging in background-cluttered space acquire food by capturing insects in aerial pursuits at forest edges, in forest gaps or by trawling insects and/or fish from water surfaces. Bats hunting in uncluttered space are fast flyers and forage on insects above the canopy. Our paucity of knowledge of aerial insectivorous bats likely stems primarily from logistical constraints, as standard mist net protocols are inadequate for a comprehensive assessment of aerial insectivores (O'Farrell and Gannon, 1999; Kalko et al., 2008). Although high forest strata have been intensively surveyed with mist nets (e.g. Kalko and Handley, 2001; Bernard, 2001; Meyer and Kalko, 2008), it is acknowledged that richness and abundance of aerial insectivores was underestimated because these bats avoid mist nets effectively or fly above the canopy where sampling is unfeasible. With advancements made in monitoring aerial insectivores through the use of audio recording devices, we are now able to study this diverse group in more detail (Kalko et al., 2008; MacSwiney et al., 2008) and to complement the few studies on fragmentation effects of aerial insectivorous bats (Law et al., 1999; Estrada et al., 2004).

Using state of the art acoustic monitoring techniques, our objective here was to determine the effects of forest fragmentation, in terms of remnant size and isolation, on species richness and ensemble structure of aerial insectivorous bats within a land-bridge island system of high fragment-matrix contrast in Gatún Lake, Panama. In a previous mist-netting study in the same fragmented landscape, Meyer and Kalko (2008) documented profound differences in phyllostomid species richness, assemblage structure and ensemble composition between islands and mainland forest sites. Consistent with the findings by Meyer and Kalko (2008) and in line with classic island biogeography theory and previously described responses of animals to tropical forest transformation, we hypothesized that aerial insectivorous bats will show changes in species richness, composition, and count abundance at the ensemble and species level. In particular we tested the following predictions:

(1) We expected that bats depending on forested habitats for foraging, i.e. hunting in background-cluttered and highly-cluttered space (hereafter referred to as forest species) to decrease in richness and count abundance on islands in relation to island size and isolation.

(2) In contrast, we predicted that species hunting in open space or over water (hereafter referred to as open space/over water foragers) will not exhibit a strong decline in species richness and count abundance in fragments because of their capability to cover long distances due to their flight behavior.

(3) We also expected rather similar ensemble structures and species richness at sites with similar degrees of isolation, size and vegetation structure.

(4) We anticipated lower richness, count abundance and feeding activity at continuous forest edge sites for forest species because previous studies have shown that biotic and abiotic factors can modify forest structure and available resources at edges (Laurance et al., 2002).

2. Methods

2.1. Study area and sampling sites

Our study was conducted on islands in Lake Gatún and on adjacent mainland peninsulas in the Barro Colorado Nature Monument (BCNM, 9°09′N, 79°51′W, Fig. 1), a 5400 ha biological reserve that is contiguous with Soberanía National Park (22,000 ha). Islands are former hilltops, isolated by the creation of the Panama Canal in 1914. Forests classify as semi-deciduous, lowland tropical moist forest (Holdridge, 1967). Climate is strongly seasonal (total rainfall: 1600 mm) with a rainy season from April or May to December and a marked dry season the rest of the year (Windsor, 1990). The forest on the mainland peninsulas is mature forest (400–600 years) interspersed with small patches of older secondary forest (about 80–100 years) (Leigh, 1999). Most islands are covered with low-stature, secondary forest with high levels of disturbance due to strong and persistent dry-season trade winds, strongly impacting forest structure and dynamics (Leigh et al., 1993; Adler, 2000). There are no light sources (e.g. canal buoys) close to the study sites which might have attracted insects and, subsequently, bats feeding on them. We never saw bats foraging near the buoys nor did we register large swarms of insects around them. Moreover, there were also no large artificial, man-made structures near the study sites. The closest were the lab facilities on Barro Colorado Island or rural areas at a distance of more than 3–5 km from our study sites.

Acoustic surveys were conducted at the same sites used by Meyer and Kalko (2008) in an extensive mist-netting study with the exception of three islands that were not included here due to logistical reasons. Following Meyer and Kalko (2008) we assigned islands to four categories, depending on their shortest distance to the mainland and size: "near" (<*ca.* 500 m) versus "far" (>*ca.* 1500 m), "large" (11.4–50 ha) versus "small" (2.5–5.9 ha) (Table 1, Fig. 1). Continuous forest sites within the BCNM (pensinsulas Bohio, Gigante and Peña Blanca, Fig. 1) were classified as "mainland interior" (>300 m away from shore) and "mainland edge" (next to the shore), respectively. Edge effects in the interior sites are considered to be low at the chosen distance (Laurance et al., 2002; Harper et al., 2005). We adapted our acoustic monitoring scheme to the configuration of the netting plots used by Meyer and Kalko (2008), i.e. one semi-rectangular plot of ca. 0.5 ha per site. Specifically, we used a total of seven recording stations, six stations spaced at equal distances along the perimeter of these plots with their positions matching the ground net locations and one additional station inside each plot corresponding to the location of the canopy net.

2.2. Sound recordings and analysis

Prior to the onset of the surveys, a reference library of echolocation calls from the species known to be present in the BCNM and surroundings was built based on calls compiled over more than