Fear or food? Prey availability is more important than predation risk in determining insectivorous bat responses across a disturbed tropical forest landscape

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Abstract

Habitat disturbance affects, directly or indirectly, the predation risk and food available to animals. One group of animals that may be negatively affected by habitat disturbance are forest-dependent aerial insectivorous bats, especially in the Amazon rainforest, where forest clearance and degradation continue unabated. However, we still have a limited understanding of the mechanisms underlying the negative effect of habitat disturbance on forest aerial insectivorous bats. Evaluating the changes in prey-predator interaction in disturbed habitats can provide helpful information for protected area management. We evaluated how predation risk, insect biomass, and moonlight intensity affect bat activity levels in continuous primary and disturbed forests (fragments and secondary forest) at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil. We sampled bats using autonomous ultrasound recorders in continuous forest, forest fragments, and secondary forest. To assess insect biomass, we placed malaise traps close to the recorders and conducted a playback experiment consisting of owl calls to assess the influence of increased predation risk by natural predators on bat activity. We found that continuous forest had higher bat activity than fragments and secondary forest, probably reflecting higher insect biomass in continuous primary forest compared to secondary forest. Insect biomass was the best predictor of activity in disturbed habitats compared to predation risk and moonlight. Predation risk did not modulate bat activity in any habitat type. The effect of moonlight intensity on activity was only apparent in three species in different habitats. Our results suggest that these responses were related to the abundance of specific insect orders and not predation risk. Overall, our findings emphasize the importance of evaluating the effects of prey-predator interactions on the distribution of bats in disturbed tropical forests, as habitat disturbance can negatively affect lower trophic levels and consequently influence not only bats but other insect consumers.

Keywords Acoustic sampling; Bat conservation; Fragmentation; Temporal activity; Tropical ecology

Introduction

Prey-predator interactions involve minimizing exposure to predators and maximizing feeding efficiency (Lima 1985; Pyke 2010). Antipredator decisions by prey can involve predator behavior and prey behavior. Predators are categorized as either ambush predators (i.e., sit-and-wait strategy) or cursorial predators (i.e., active hunting strategy) (Gable et al. 2021; Schmitz 2008). Prey can flee from ambush predators (i.e., evasion) or hide from cursorial predators (using cover, crypsis, or freezing) (Sih et al. 1998; Wirsing et al. 2010). For prey species that use cover to reduce exposure to a predator, environmental variables such as vegetation density and habitat quality can be key factors determining habitat use (Lima and Dill 1990; Massé and Côté 2006). High vegetation density can limit prey visibility for predators that use vision to forage, and prey also find more places to hide (Lima and Dill, 1990; Riginos and Grace, 2008). Moreover, lower-quality habitats can increase the predation risk for prey, resulting in altered foraging patterns or behaviorally-mediated trophic cascades (Palmer et al. 2022). Thus, heterogeneous landscapes can create different situations of fear and forage (Kotler and Brown 1999), but, intuitively, lower-quality habitats can negatively affect predators and prey compared to higher-quality habitats.

Lower-quality habitats may originate from human activities, such as deforestation, fragmentation, and forest degradation, which are increasing across the tropics. One of these human-disturbed habitats is secondary regenerating forest, which is rapidly expanding in the Brazilian Amazon, amounting to an area of 180,215 km^2 (Smith et al. 2021). These disturbed habitats differ from preserved habitats in a range of characteristics, such as vegetation structure and abiotic and biotic conditions, which can alter prey availability and foraging opportunities for predators (Haddad et al. 2015; Michalko et al. 2021). Indeed, degraded forests, including tropical regenerating forests have lower biodiversity than primary forests (Gibson et al. 2011), consequently affecting the availability of different prey species for forest predators. Small forest fragments surrounded by a low-contrast matrix, for example, can suffer from edge effects, including reduced forest cover, which exposes prey species to greater predation risk relative to that experienced in larger fragments and continuous primary forest

(Morrison et al., 2010; Tufto, Linnell, & Andersen, 1996). The abundance and biomass of moths are positively and strongly determined by local plant diversity and vegetation complexity (Alonso-Rodríguez et al. 2017; Hawes et al. 2009), which can directly affect insectivorous animals such as forest-dwelling insectivorous bats (Froidevaux et al. 2021).

Aerial insectivorous bats are crucial to providing ecosystem services such as the suppression of agricultural pests and mosquitos that transmit diseases (Puig-Montserrat et al. 2020; Montauban et al. 2021; Curran et al. 2022). Forest-dwelling bat species are highly dependent on complex vegetation, providing adequate opportunities for roosting and foraging (López-Baucells et al. 2022). Most aerial insectivorous bats respond negatively to habitat disturbance, showing curtailed activity in disturbed habitats (Jung and Kalko 2010; Estrada-Villegas et al. 2010; de Araújo and Bernard 2016; Falcão et al. 2021). In the Central Amazon, the activity of some forest insectivorous species can decrease in fragments and secondary regenerating forest (Appel et al. 2021; Rowley 2022). The mechanisms that explain this reduction in aerial insectivorous bat activity in disturbed forest habitats may be related to changes in abiotic conditions, prey-predator interactions, roost availability, and mating opportunities (Kingston 2013; Arrizabalaga-Escudero et al. 2015).

Moonlight intensity, predation risk, and insect availability, directly and indirectly, influence the foraging activity of tropical bats (Saldaña-Vásquez and Munguía-Rosas 2013). In forest fragments, aerial insectivorous bats are less active on extremely bright nights than dark nights, probably due to higher vulnerability to predators when traversing the matrix (Appel et al. 2021). Observational evidence indicates that presence of diurnal predators at the entrance of bat roosts can affect the timing of emergence (Welbergen 2006) and the number of bats that emerge (Kalcounis

& Brigham 1994). However, the behavioural responses of bats to perceived nocturnal predation risk while foraging are still unclear, especially for tropical species (Lima and O'Keefe 2013). Only one study tested the risk of owls for frugivorous bats in the tropics, showing that bats decreased their foraging activity in fruit trees when stimulated by visual cues of owls (Breviglieri et al. 2013). For tropical aerial insectivorous bat species, which rely less on vision to hunt than frugivores and nectarivores, assessing the effect of vocalizing predators on activity is essential to understand habitat selection in undisturbed and disturbed habitats. Moreover, many studies suggest that insectivorous bats concentrate their activity during periods when insects are most abundant (Speakman et al. 2000; Meyer et al. 2004; Oliveira et al. 2015). Habitats with different vegetation cover and disturbance may affect the trophic interaction between bats and their prey through reduced insect availability (Treitler et al. 2016) and can provide useful information about the management of disturbed forests to promote bat activity.

In this study, we evaluated how human-modified landscapes influence the activity of seven aerial insectivorous bat species in relation to food availability, predation risk, and moonlight intensity. We acoustically quantified bat activity in the disturbed landscape of the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon, specifically in continuous forest (control) and in disturbed habitats (forest fragments and secondary forest) to examine variation in species-level activity. Playback experiments in each habitat type were conducted to determine the effect of perceived predation risk on bat activity. To assess food availability, we sampled aerial insects in the vicinity of the acoustic recorders in each habitat type and determined their biomass. We also considered moonlight intensity as a factor influencing the foraging behaviour of bats in each habitat type (Appel et al. 2021). Our general hypothesis was that the activity of aerial insectivorous bats would be highest in continuous primary forest and lower in disturbed habitats due to the higher predation risk and reduced insect biomass (Hallmann et al. 2017). Thus, across the disturbed landscape, we tested the following predictions:

(1) We anticipated that most aerial insectivorous bat species would respond to insect biomass rather than predation risk in continuous forest. By contrast, in disturbed habitats (fragments and secondary forest), most aerial insectivorous bat species would respond to predation risk more than insect biomass. These responses would reflect the higher insect biomass across the continuous forest and the greater exposure to predators in disturbed habitats due to the reduced habitat quality.
(2) We expected that the interaction of moonlight intensity with insect biomass and predation risk would not affect bat activity in continuous forest, where habitat quality and insect biomass are assumed to be higher than in disturbed habitats (Uhler et al. 2021). For the disturbed habitats, we predicted that most bat species would be negatively affected by moonlight intensity and predation risk (Appel et al. 2021).
(3) We predicted that the hourly activity of bat species would be affected by predation risk in fragments and secondary forest.

Material and Methods

Study site

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) (2°25'S; 59°50'W), located ~80 km north of Manaus, Brazil (Fig. S1), one of the world's most extensive and longest-running experimental investigations of habitat fragmentation and forest regeneration (Laurance et al. 2018). Located in Central Amazonia, the area contains lowland evergreen *terra firme* rainforest at 50 to 100 m of elevation (Laurance and Williamson 2001). The study area includes 11 forest fragments (five of 1 ha, four of 10 ha, and two of 100 ha), surrounded mainly by a matrix of secondary forest in an advanced stage of regeneration and significant extensions of continuous forest that act as experimental controls (Laurance et al. 2018). Periodically, the fragments are re-isolated by clearing the forest up to 100 meters around the fragments; the last re-isolation took place in 2014 (Rocha et al. 2017). The secondary forest is dominated by *Cecropia* spp. in areas that were only cleared and by *Vismia* spp. in areas where forest was removed, burned, and used for pasture before abandonment (Mesquita et al. 2001). The dry season typically lasts from July to November when precipitation is less than 100 mm/month and, the rainy season occurs from November to June, when precipitation can reach 300 mm/month (Ferreira et al. 2017). We estimated canopy cover using a spherical densiometer (Model C, Robert E. Lemmon, USA). In each habitat type, four readings were taken and we found that canopy cover varies little between habitat types (continuous forest interior: 91.5 ± 1.32 [mean ± SD]; fragments of 10 ha interior: 89.7 ± 0.55; secondary forest: 86.7 ± 2.82). Canopy height in the large fragments and continuous forest averages 28 m (Almeida et al. 2019), while in the well-developed secondary forest the average canopy height is 15 m (Jakovac et al. 2014; Mokross et al. 2018). In view of the limited variation in canopy cover, we assumed that moonlight penetrates into the forest similarly in all habitats.

Bat acoustic sampling and bat identification

We sampled at nine sites across the BDFFP landscape: three sites in continuous forest (Cabo Frio, Florestal and Km 41 camps), three 10 ha fragments (Porto Alegre, Colosso and Dimona camps) and three sites in secondary forest (Porto Alegre, Cabo Frio and Dimona camps) (Fig. S1). Each site was visited twice in each season (dry season of 2018 and rainy season of 2019) and the number of sampling nights varied between 18 and 30 per season in each habitat type (Tab. S1). We positioned one passive ultrasound recorders in the center of the fragments, in the secondary forest at least 500 m away from the edge of a fragment or continuous forest, and in the interior of continuous forest 1000 m away from the edge. At each site, we installed an automatic ultrasound recorder (Song Meter SM2Bat+) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, Inc., USA) placed at a height of 1.5 m above the ground. The recorders were programmed to passively register bat activity in real time, with a full spectrum resolution of 16 bit, a high-pass filter set at fs/32 (12 kHz), and an adaptive trigger level relative to noise floor of 18 SNR. Bat activity was recorded between 17:30 and 06:30 for two to four consecutive nights per visit, totalling at least 40 nights per sampling site (Tab. S2). We recorded for 138 nights, totalling 1,794 recording hours.

Each night's recordings were split into five-second long segments using Kaleidoscope software (Wildlife Acoustics, Inc.,, USA) and we defined a bat pass as a five-second segment with at least two recognizable search-phase calls per species (Appel et al. 2019; Gomes et al. 2020). We manually identified the bat passes to species level or sonotype level when it was impossible to assign the call to a particular species. Identification followed the acoustic key in López-Baucells et al. (2016). For manual identification of each recording, we used Kaleidoscope Software (version 4.0.4). We calculated bat activity as the sum of five-second segments with bat passes per night (nightly activity) and per hour (hourly activity).

We identified ~39,800 bat passes of 13 aerial insectivorous bat species and 10 sonotypes. To minimize potential detection biases we focused on species that were detected in at least 45% (63 nights) of the total number of recording nights. Thus, we selected seven species for analysis: *Pteronotus alitonus*, *P. rubiginosus* (revised by Pavan et al. 2018), *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura* and *Peropteryx kappleri* (Table S3).

Predator call experiment

To test if predation risk influences the activity of aerial insectivorous bats, we performed playback experiments with three treatments at all sites: a) playback of owl species calls; b) broadcasting noise treatment; c) without owl calls or noise (control treatment). Each night of acoustic sampling, we ran one of the treatments, maintaining an order that did not repeat the treatment of the previous night. Owl calls and noise sound were played using a JBL (Clip 2) speaker connected to a portable battery and a cell phone that contained one playlist. The speaker was installed five meters away from the ultrasound recorder at a height of 1.5 m above ground level. Predator and noise treatments lasted for the same duration of the deployment of the ultrasound recorder (17:30 to 06:30) and were broadcasted every 15 minutes for a duration of one minute. This temporal vocal activity pattern of owls agrees with that observed for owl species at the BDFFP (Bonamoni *et al.*, *personal communication*). Indeed, we used a different playlist order of owl species calls to avoid repetition of the same playlist from the previous night. We used noise treatment to validate the treatment of owl calls, if bats respond to noise this means that a possible response to the owl calls is not validated. We had at least 11 nights for each treatment in each habitat type (Tab. S2).

For the treatment of owl calls, we selected the following species that were reported to prey on bats and that were previously registered at the BDFFP (Bonamoni 2013): *Lophostrix cristata*, *Megascops watsonii*, *Strix huhula*, *Strix virgata* and *Pulsatrix perspecillata* (Almeida et al. 2021; Cadena-Ortiz et al. 2013; Carvalho et al. 2011; Rocha and López-Baucells 2014; Serra-Gonçalves et al. 2017). Owl calls were obtained from the Xeno-canto website (https://xeno-canto.org/), which is an open bird song repository. The owls' vocalization frequency range (8-20 kHz) was within the hearing capacity of the bat species evaluated here (*Pteronotus*: 10-112 kHz, Kössl and Vater 1996; emballonurid species such as *S. bilineata* and *S. leptura*: 5-100 kHz, Lattemkamp et al. 2021). We used a broadcasting noise in the noise treatments that contains all frequencies across the spectrum of audible sound in equal measure ranging between 0 and 8268.8 kHz. This noise was obtained from the SimplyNoise website (https://simplynoise.com/). This broadcasting noise has been used in studies which tested the influence of noise on animal activity (Medeiros et al. 2017).

Nocturnal insect sampling

Nocturnal flying insects (hereafter insects) were sampled at each site alongside acoustic sampling of bats and predator experiments. To avoid possible biases associated with the use of light traps while recording bats (Froidevaux, Fialas, & Jones, 2018), we used Malaise traps to capture insects (1.60 m height x 1.50 m length). These traps collect a great variety and abundance of insects eaten by bats such as Diptera, Coleoptera, Lepidoptera, Hymenoptera, Hemiptera and Orthoptera (Table S4). We installed four malaise traps around the ultrasound recorder whereby each malaise trap was placed 20 meters from the recorder in the four cardinal directions (Fig. S2). To collect only nocturnal insects, we installed the traps before sunset (17:30) and took them down at sunrise (06:00).

Insects were preserved in bottles containing 90% alcohol, which were labeled and taken to the Animal Biology Laboratory of the Federal University of Amazonas (UFAM) for sorting and identification. Species identifications were made by UFAM and National Institute for Amazonian Research (INPA) entomologists and identified to order level based on identification keys by Rafael et al. (2012). For each insect order, we counted the number of individuals and weighed them to estimate the total biomass of insects per night. To remove excess alcohol from the insects, we dried them with filter paper and weighed each insect on a precision balance (precision limit 0.0001 g; Ohaus Discovery, Pine Brook, New Jersey). We estimated the average insect biomass per night by dividing the mass by the number of insects collected (Oliveira et al. 2015).

Moonlight intensity

Moonlight intensity for each night was calculated using the “sunmoon” software (Kyba et al. 2020), a robust method for quantifying the amount of sunlight reflected by the moon. This software employs the illuminance model proposed by Janiczek and DeYoung (1987). We used the percentage of moonlight intensity instead of the moon phase because moonlight luminosity varies greatly within the same moon phase (Appel et al. 2017; 2021). At each site and for each treatment, we sampled nights with different percentages of moonlight intensity to cover the whole gradient in variation of moonlight intensity (0 to 100%).

Data analysis

To understand if bat activity levels and insect biomass vary between habitat types, we tested the effect of habitat type (continuous, fragment and secondary forest) on total and species-specific bat activity levels and insect biomass. For the bats, we performed generalized linear mixed models (GLMMs) in the R package “glmmTMB” (Bolker et al. 2020) and the response variable was the number of bats passes per night, all species combined and per species. Models were fitted using a negative binomial distribution and we used zero-inflated models when the species distribution showed a signal of zero inflation (Zuur et al. 2009). To account for the temporal autocorrelation in the data, habitat type was the categorical fixed effect and, we used sampling night nested within research camp as a random effect. To compare activity levels between fragments and secondary forest, we evaluated these differences using least-squares means (predicted marginal means) analysis with the lsmeans package (Lenth 2016). For insect biomass, we tested the influence of habitat type on insect biomass using Gardner-Altman estimation plots and evaluated statistical differences using non-parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95% confidence intervals for the difference of means with the package “dabestr” (Ho et al. 2019). The statistical significance of differences in insect biomass between habitat types was inferred based on the lack of overlap in the frequency distributions of the data.

As the bat activity levels and insect biomass vary between the habitat types, we performed GLMMs for each bat species and total bat activity in each habitat type. We conducted these analyses rather than putting all the variables (including habitat type) into one model, because we chose to understand what are the variables that drive bat activity in each habitat type and to avoid overparameterization and collinearity of models with many interactions (Grueber et al. 2011). To test the effects of insect biomass and owl calls on bat activity in each habitat, we also performed GLMMs using “glmmTMB”. First, we made a model testing the additive effects of insect biomass and playback treatment (control, noise, and owl call) on bat activity levels. Second, we tested the additive effects of insect biomass and moonlight intensity and their interactive effect on bat activity levels. The predictors (insect biomass and moonlight intensity) of this second model were standardized to a mean of 0 and an SD of 1 to facilitate a comparison of their relative effects. Third, we made a model with the additive effects of playback treatment and moonlight intensity, and their interactive effect on bat activity. In the third model, we did not standardize the predictors due to the categorical predictor of playback treatment. For all models, we used sampling night nested within the research camp as a random effect to account for the temporal autocorrelation in the data and the negative-binomial distribution of response variables. For the analysis of species that included insects as a predictor, we used only the insect orders that each bat species consumes according to the literature (Tab. S5). The residuals of all models were checked using the DHARMa package (Hartig 2022) and we tested overdispersion and zero inflation with the same package.

Differences in hourly activity between owl call playback treatment and control treatment for each habitat type were assessed using Kolmogorov-Smirnov 2-sample tests. Bat activity of each species was divided into 12 intervals (hourly intervals). For comparisons between these two treatments, we used data from 36 nights in continuous forest (17 nights of owl calls, 19 of control), 30 nights in fragments (13 nights of owl calls, 17 of control), and 30 nights in secondary forest (15 nights of owl calls, 15 of control). All analyses were performed in the software R 4.02. and R Studio 4.0.2 (R Core Team 2021; Rstudio Team 2021).

Results

Effects of habitat type on bat activity and nocturnal insect biomass

Total bat activity was higher in continuous forest compared to disturbed habitats (Fig. 1), with activity levels being 2.06 and 1.84 times higher in continuous forest compared to fragments and secondary forest, respectively (Tab. S3). The most negative effects on species-specific activity responses were observed in the fragments. The activity of two species (*C. maximiliani* and *C. brevirostris*) was lower in fragments than continuous forest (Fig. 1). Only *P. rubiginosus* activity was lower in secondary forest than continuous forest, in contrast to *P. alitonus* and *P. kappleri* which showed higher activity in secondary forest than continuous forest (Fig. 1). When comparing fragments with secondary forest, four species (*P. alitonus, C. maximiliani, C. brevirostris* and *P. kappleri*) had higher activity in secondary forest while only *P. rubiginosus* had higher activity in fragments (Tab. S6).

We sampled a total of 46,401 nocturnal insects and Diptera represented 61.7% of all sampled individuals, followed by Hymenoptera with 17.13%, Collembola with 9.2%, and Lepidoptera with 3.7% (Tab. S4). The remaining orders (e.g., Hemiptera, Coleoptera, Orthoptera, Isoptera, Blattodea, Trichoptera) accounted for 9% of total insects. Nocturnal insect biomass (based on insect orders relevant to the diet of most bat species; *P. alitonus, P. rubiginosus, S. bilineata, C. maximiliani, C. brevirostris* and *P. kappleri*) in secondary forest was on average 3.1 times lower than in continuous forest (Fig. 2). No differences in insect biomass were found between continuous forest and fragments (Fig. 2; Tab. S7). On the other hand, the biomass of insects featuring in the diets of *S. bilineata*, *C. maximiliani,* and *P. kappleri* was on average two times lower in the secondary forest compared to fragments (Fig. 2).

Effects of insect biomass and owl call on bat activity in each habitat type

We found a positive relationship between activity of four species (*P. alitonus*, *P. rubiginosus*, *S. bilineata* and *C. brevirostris*) and insect biomass in continuous forest (Fig. 3A). Conversely, in secondary forest, total bat activity and activity of *P. alitonus* were negatively related to insect biomass (Fig. 3A). We did not find any influence of owl call playback on bat activity in any habitat, except for *P. kappleri* which responded negatively to the owl calls, but also to noise, indicating that this species is affected by any type of sound, not necessarily the predator call (Fig. 3A). We also did not find any relationship between insect biomass and owl call with bat activity in the fragments (Fig. 3A).

Effects of moonlight intensity, insect biomass, and owl call on bat activity

Only three bat species responded to moonlight intensity when we included insect biomass in the GLMM models (Fig. 3B). In continuous forest, only *C. maximiliani* was less active during brighter nights with greater insect biomass (Fig. 3B). In fragments, *P. alitonus* reduced activity with increasing moonlight intensity and *P. kappleri* was more active during brighter nights with greater insect biomass (Fig. 3B). In secondary forest, only *P. rubiginosus* was less active on brighter nights with lower insect biomass (Fig. 3B).

There were no significant effects of moonlight and owl call playback on bat activity in any habitat (Fig. 3C). The only significant result (*P. rubiginosus* in secondary forest) was associated with noise and therefore not considered (Fig. 3C).

Effects of owl call on hourly bat activity in each habitat type

In continuous and secondary forest, bat activity for all species combined was significantly greater during nights without owl calls than those with owl call playback, particularly in the early evening (Fig. 4). However, at the species level, hourly activity did not differ between nights with owl calls and control nights, irrespective of habitat type (Fig. 4).

Discussion

At the BDFFP, there is growing research into understanding how forest disturbance affects the functional, taxonomic, and behavioral responses of aerial insectivorous bats (López-Baucells et al. 2019, 2021, 2022; Meyer et al. 2016; Núñez et al. 2019; Yoh et al. 2022). Several studies have shown that some Amazonian aerial insectivorous bats are particularly vulnerable to habitat disturbance and fragmentation, especially understory forest specialists (Appel et al. 2021; Núnez et al. 2019; Colombo et al. 2022; Yoh et al. 2022). However, the mechanisms that explain why these species are sensitive to habitat disturbance are unknown. Our results indicate that predation risk does not modulate the activity of understory aerial insectivorous bats in disturbed habitats and that the higher activity in continuous forest is related to higher insect biomass. We also found that moonlight does not intensify the predation risk effect and does not interfere with insect consumption in preserved and disturbed habitats.

In agreement with our predictions, the total activity of aerial insectivorous bat species was negatively affected by habitat disturbance. Our results suggest that total activity in disturbed habitats (fragments and secondary forest) is half that observed in continuous forest. The reduced activity in human-disturbed habitats especially for forest-dependent aerial insectivorous species has commonly been reported (Estrada-Villegas et al. 2010; Falcão et al. 2021; Meyer et al. 2016), and this might be caused by a decrease in resources, such as roosts, food and safe environments for foraging (Bernard and Fenton 2002; Evelyn et al. 2004; Pereira et al. 2018). As we found, insect biomass was higher in continuous forest than secondary forest but is similar in fragments and continuous forest. Thus, greater availability of insects in continuous forest probably creates better foraging opportunities for aerial insectivorous bats, as has been reported in other studies (Oliveira et al. 2015; Ketzler et al. 2018; Put et al. 2018; Scanlon and Petit 2008). This difference in insect biomass between continuous forest and secondary forest likely reflects differences in plant species composition (Alonso-Rodríguez et al. 2017; Hawes et al. 2009). Herbivorous insects often consume specific plant genera or species (Haddad et al. 2009), so well-preserved habitats commonly have higher diversity and biomass of vegetation-associated insects (Ebeling et al. 2019; Welti and Kaspari 2020). Secondary forests dominated by *Vismia* have lower plant diversity than continuous forest (Jokovac et al. 2014) and consequently, insects are probably less diverse and may have lower dry body mass (Salomão et al. 2018).

Fragments had more species with negative activity responses than secondary forest, and five species had lower activity in fragments than secondary forest. This result is different from what we expected, because based on intensive acoustic sampling conducted at the BDFFP between 2011 and 2013 we showed that most aerial insectivorous species were less active in secondary forest (Appel et al. 2021). This was probably due to the reisolation of the fragments in 2014 (Rocha et al. 2017). The acoustic sampling of the present study (2018-2019) was done in fragments surrounded by a secondary forest at an early stage of regeneration compared to 30 years of matrix regeneration in the previous study (Appel et al. 2021; López-Baucells et al. 2022). Fragment reisolation thus had substantial negative effects on total activity of aerial insectivores, even after just four years of forest regeneration.

Our findings suggest that insectivorous bats exhibit species- and guild-specific responses to forest disturbance. Such responses may be affected by their foraging strategy, wing morphology, echolocation call structure and forest strata preference (Alpízar et al. 2019; Gomes et al. 2020; Colombo et al. 2022). *Pteronotus alitonus* was clearly more active in secondary forest than in continuous and fragment forest. This species has intermediate values of aspect ratio and wing loading, showing a flexible and adaptable flight (Marinello and Bernard 2014) and at the BDFFP is known as a species with no preference for any habitat type or fragment size (Rowley 2022; Yoh et al. 2022). *Peropteryx kappleri* also had increased activity in secondary forest, and this is probably related to its strategy of being an edge forager and its canopy preference (Gomes et al. 2020; Yoh et al. 2022). Secondary forests at the BDFFP are less tall than continuous forest (<15 m), so vertical stratification is less pronounced and possibly the recorders in these regenerating forests detect more of this aerial insectivorous species.

As we expected, most aerial insectivorous bat species responded to insect biomass rather than predation risk in continuous forest. Bat species can maximize the energy gain with higher insect biomass and minimize exposure with the protective cover of continuous forest, therefore the benefits outweighed the risk of predation (Jung and Kalko 2010; Rydell et al. 1996). However, contrary to our expectations, predation risk did not affect bat activity responses in disturbed habitats. Our results indicate that owl calls do not alter aerial insectivorous bat activity in any habitat type. A lack of response of bats to owl calls was also found for temperate species (Janos and Root 2014) and for neotropical frugivorous species (Breviglieri et al. 2013). There are several possible reasons for this: (1) Owls use their vision to hunt, and they cannot hear ultrasound calls emitted by bats as the upper limit of hearing frequency of owls is between 7 and 18 kHz (Beason 2004; Konishi 1973). Thus, the perception and pursuit of prey by owls in dense vegetation can be hampered (Apolloni et al. 2017). The response of bats to owls presumably might be higher in open areas such as pastures and agricultural lands. (2) Bats probably perceived the owl calls as nonthreatening nocturnal noise in forested sites (Janos and Root 2014) as the vocal activity of owls is not associated with hunting, but with territorial advertising and mate attraction (Penteriani and Delgado 2009); (3) The acoustic stimulus is not strong enough to trigger anti-predator responses in bats compared to other stimuli such as visual cues, odor, movement and vocalization of an attacked bat (Breviglieri et al. 2013; Fenton et al. 1994). We only used owl calls as predation risk stimulus and we evaluated only the changes in activity as antipredator response of bats, thus further investigation is needed to test other stimuli (Baxter et al. 2006), predators, and different response measures of bats such as changes in the timing of emergence from roosts (Petrzelkova and Zukal 2003) and mobbing behavior as antipredator adaptation (Knörnschild and Tschapka 2012).

Our results also show that variation in moonlight intensity has a weak effect on bat activity and does not suppress the activity of most bat species in disturbed habitats. Our previous study showed that variation in moonlight intensity between nights affects aerial insectivorous bat activity in disturbed habitats very little (Appel et al. 2021). However, in the present study, three bat species responded to moonlight in association with insect biomass, but no species responded to moonlight associated with predation risk. These results suggest that insect availability may indirectly influence the activity of some aerial insectivorous species on nights with different moonlight intensities (Lang et al. 2007). Insect orders eaten by *P. alitonus* and *P. rubiginosus* decrease with moonlight in fragments and secondary forest (linear regression analysis: estimate = -0.002; t = -5.24; P <0.0001 for fragments, and estimate = -0.002; t = -6.47; P <0.0001 for secondary forest). By contrast, Lepidoptera were more abundant at greater moonlight intensities in fragments, which could explain the higher activity of *P. kappleri* on bright nights in fragments (estimate = 0.006; t = 4.18; P <0.001). For *C. maximiliani*, we found no statistical effect of moonlight for the insect orders consumed by this species (Lepidoptera and Coleoptera; estimate = 0.001; t = 1.17; P <0.65), and maybe this reflects the lack of knowledge about other insects that *C. maximiliani* eats since we only found two studies (Starrett and Casebeer 1968; Woodman 2003).

We found a reduction of hourly total activity on nights with owl calls in continuous and secondary forests. In continuous forest, total bat activity was lower at the beginning of the night and 2 and 3 pm on nights with owl calls compared to control nights. In secondary forest, total bat activity on nights with owl calls was also slightly reduced the whole night compared to control nights. This provides some evidence that tropical aerial insectivorous bats may change activity in response to predation risk for short periods throughout the night. Some bat species tend to emerge later when predators are present (Russo et al. 2011; Welbergen 2006). Bats need to feed at the beginning of the night to meet their energetic demands, but when predation risk is high, they can adjust and distribute their activity over the course of the night, especially gleaning insectivorous species whose food is evenly distributed over the night (Kalko et al. 1999; Weinbeer and Kalko 2004). However, we did not find a species-specific response, indicating that the activity at the assemblage level often does not correspond to the activity of the species that compose it.

Despite species-specific differences, in general, total bat activity was higher in continuous forest compared to disturbed habitats, likely a consequence of the higher insect biomass of continuous forests. The effects of habitat disturbance on aerial insectivorous bat activity appeared to be more related to insect biomass than predation risk and moonlight. Therefore, the regeneration of the matrix probably will increase available insect biomass and consequently bat activity over time. Nonetheless, we should strongly prioritize areas that constitute hotspots of nocturnal insect biomass as protected reserves for bat conservation, since changes in insect biomass may have cascading effects on bat activity (Froidevaux et al. 2021). Many birds and other vertebrates are linked to the prey of insectivorous bats, so the conservation of these foraging habitats ensures the nocturnal trophic structure is preserved (Arrizabalaga-Escudero et al. 2015). Otherwise, other characteristics such as vegetation structure, terrain elevation, forest composition, weather conditions, and roost quality can shape bat activity (Barros et al. 2014; Meyer et al. 2004; Russo et al. 2016; Cabral et al. 2023) in disturbed habitats, and they need to be considered in further investigations to better understand the local needs of bats.

Finally, our study highlighted the importance of continuous primary forest for forest aerial insectivorous bat species and to preserve their ecological functions, such as insect control. Aerial insectivorous bats from the Brazilian savanna consume a significantly greater number of pest insects than of other functional groups (e.g., pollinators, predators, parasitoids) (Aguiar et al. 2021). According to our literature review, there are no studies on the diet of aerial insectivorous bats in the Brazilian Amazon, so we recommend that future studies address this knowledge gap. Even in low-contrast matrix landscape such as the BDFFP, substantial changes in insect availability influence bat activity and probably the activity of several other insect consumers. In conclusion, conservation efforts for tropical aerial insectivorous bats should concentrate on the maintenance of mosaic landscapes which encompass large tracts of continuous forests.

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Authors contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Giulliana Appel. The first draft of the manuscript was written by Giulliana Appel and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare that no competing interests exist.

Consent to participate All authors gave consent to participate.

Consent for publication All authors gave consent for publication

Legends

Fig. 1. Comparison of the activity of each bat species between continuous forest (green boxes), fragments (yellow) and secondary forest (orange) at the BDFFP. Significant comparisons ($P \leq 0.05$) are indicated with '*'.

Fig. 2. Comparison of the aerial insect biomass (g) per bat species diet between continuous forest (green dots), fragments (yellow) and secondary forest (orange) at the BDFFP. Significant comparisons ($P \leq 0.05$) are indicated with '*'.

Fig. 3. The first heatmap (A) depicts the significant results of a GLMM evaluating the effects of insect biomass, owl calls and noise on bat activity for each bat species and habitat type. The second heatmap (B) shows the significant results of a GLMM assessing the effects of insect biomass, moonlight, and their interaction on activity for each bat species and habitat type. The third heatmap (C) depicts significant results of a GLMM on the effects of owl calls, moonlight and their interaction on activity for each bat species and habitat type. The colour gradient indicates the magnitude of a predictor's estimate for individual response variables. Blue boxes indicate significant

negative effects, red boxes indicate significant positive effects and grey boxes indicate lack of statistical significance. ‘*’ $P \leq 0.05$, ‘**’ $P < 0.01$ and ‘***’ $P < 0.001$.

Fig. 4. Hourly activity of aerial insectivorous bat species in each habitat type (continuous, fragments and secondary forest) on control nights (without sound) and nights with owl calls. Black bars denote control nights, grey bars depict nights with owl calls. The solid bar is the average activity, and the dotted line is the standard deviation of activity. ‘*’ indicates a significant difference between the treatments based on Kolgomorov-Smirnov 2-sample tests ($P \leq 0.05$).

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