1   **Habitat disturbance trumps moonlight effects on the activity of tropical insectivorous**

2   **bats**

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4   Giulliana Appel[1,2], Adrià López-Baucells[2,3,4], Ricardo Rocha[2,4,5,6], Christoph F. J. Meyer[2,7]

5   and Paulo Estefano D. Bobrowiec[1,2]

6

7   [1] Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia,

8   Manaus, 69080-971, Brazil

9   [2] Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da

10   Amazônia, Manaus, 69067-375, Brazil

11   [3] Bat Research Group, Granollers Museum of Natural Science, Granollers, 08402, Spain

12   [4] Centre for Ecology, Evolution and Environmental Changes, University of Lisbon, Lisbon,

13   1749-016, Portugal

14   [5] CIBIO/InBIO-UP, Research Centre in Biodiversity and Genetic Resources, University of

15   Porto, Vairão, 4485-661, Portugal

16   [6] CEABN-InBIO, Centre for Applied Ecology "Prof. Baeta Neves", Institute of Agronomy,

17   University of Lisbon, Lisbon, 1349-017, Portugal

18   [7] School of Science, Engineering and Environment, University of Salford, Salford, M5 4WT,

19   UK

20

21   **Abstract**

22   Changes in moonlight intensity can affect predation risk and induce changes in habitat use

23   and activity of nocturnal species. However, the effect of moonlight on animal activity is

24   rarely evaluated in human-modified landscapes and can be of vital importance to understand

25   possible changes in ecosystem services provided by light-sensitive taxa, such as insectivorous

26   bats. Fragmentation changes forest structure and affects light penetration across the

27   landscape. In this case, the effects of fragmentation on bat activity can be modulated by

28   cyclical variations of moonlight intensity. We acoustically quantified the activity of nine

29   aerial insectivorous bat species in relation to moonlight at the Biological Dynamics of Forest

30   Fragments Project, Central Amazonia. We aimed to understand species-level variation in

31   activity across habitats (continuous forest, fragments and secondary forest) at different

32   temporal scales: lunar cycle, dark *vs* bright nights, and within nights. Amazonian aerial

33   insectivorous bats responded more to habitat type than to moonlight, with two and six species

34   showing reduced activity in fragments and secondary forest, respectively, compared to

35   continuous forest. The lower activity in secondary forest suggests that despite ca. 30 years of

36   secondary forest regeneration, it is still less attractive as foraging habitat. An interactive

37   effect of habitat type and moonlight on bat activity was most evident when contrasting dark

38   and bright nights. Our results indicate that fragments have reduced bat activity on extremely

39   bright nights, probably due to higher predation risk in small fragments. Species that emit

40   constant-frequency calls (*Pteronotus* spp.) were the ones that most modulated their responses

41   to habitat disturbance and moonlight. Otherwise, moonlight had little effect on hourly activity

42   levels, irrespective of habitat type. Moonlight is capable of modulating the responses of some

43   bat species in disturbed habitats, particularly in fragments.

44

45   **Key-words:** Acoustic monitoring; Predation risk; Neotropical bats; Amazonian forest;

46   Secondary forest

Introduction

Anthropogenic habitat loss and fragmentation are key drivers of biodiversity change and erosion of ecological processes (Barlow *et al.*, 2016; Pfeifer *et al.*, 2017), especially in species-rich tropical regions such as the Amazon rainforest (Betts *et al.*, 2019). Worryingly, forest fragmentation in the Brazilian Amazon is progressing faster than ever; in 2017, there was an increase of nearly 70% in the number of fragments (Montibeller *et al.*, 2020) and this trend can be assumed to have worsened due to the high levels of forest loss in 2018-19 (Barlow *et al.*, 2020). Forest fragmentation results in the formation of isolated patches, surrounded by an anthropogenically modified matrix (Haddad *et al.*, 2015). The type of human-made matrix can act as selective filter for the movements of species (Watling *et al.*, 2011), altering the abundance, composition, phylogenetic, and functional diversity of animal assemblages (Mendenhall *et al.*, 2014; Aninta *et al.*, 2019; Rutt *et al.*, 2020).

Risk of predation is a major determinant of habitat use by animals (Atkins *et al.*, 2019; Pringle *et al.*, 2019). For nocturnal species, moonlight is an important source of information that affects foraging habitat selection (Waap *et al.*, 2017). Prey species commonly curtail their activity under bright moonlight so as to reduce the probability of predation by visually oriented predators (Navarro-castilla & Barja, 2014; Miranda et al., 2020). On the other hand, predator species can more easily locate prey under brighter conditions and thus increase their activity to maximize hunting success (Pratas-Santiago *et al.*, 2016; Bhatt, Sarma & Lyngdoh, 2018). However, species that are both prey and predators need to strike a balance between guaranteeing high foraging success and predator avoidance (Penteriani *et al.*, 2011; Linley *et al.*, 2020).

An increase in the perceived risk of predation during moonlit nights can force prey species to forage in cluttered habitats such as primary forest, in which dense canopies limit the amount of moonlight reaching the understory (Gigliotti & Diefenbach, 2017). However,

moonlight exposure in disturbed landscapes may differ from that in continuous primary

forest. Canopy openness in forest fragments and continuous forest may be similar (Almeida

et al., 2019; Rocha *et al.*, 2020), resulting in comparable levels of moonlight reaching the

undergrowth and consequently predation risk. However, the foraging area of a species may

often be larger than the fragment area, forcing the animals to forage at fragment edges and in

regrowth vegetation where exposure to bright light levels during moonlit nights is greater

(Bernard & Fenton, 2003). Therefore, relative to continuous forest, predation risk can be

expected to be higher in smaller fragments and in the surrounding matrix (Bowers & Dooley,

1993; Rocha *et al.*, 2020).

Bats are a group of essentially nocturnal animals which provide vital functions in the

maintenance of tropical ecosystems through pollination, seed dispersal and insect population

suppression (Kunz *et al.*, 2011). Studies involving the effect of moonlight on bats go back a

considerable time, in fact the term "lunar phobia" was coined by Morrison (1978) for

Neotropical frugivorous bats. Lunar phobia is a behavioural response to increased moonlight

intensity and is probably an adaptation for reducing exposure to visually orientated nocturnal

predators (Morrison 1978; Haeussler & Erkert, 1978). For aerial insectivorous bats, the

relationship with moonlight is more complex because they simultaneously face the trade-off

of being both prey and predator (Holland *et al.*, 2011; Roeleke *et al.*, 2018; Vásquez, Grez &

Pedro, 2020). In Amazonian bats, moonlight seems to have species-specific effects, with

some species either increasing or decreasing their activity in brighter nights, while others are

unaffected (Appel *et al.*, 2017).

Although there are many studies that evaluated the effect of moonlight on aerial

insectivorous bat activity, these studies are concentrated in temperate regions (Saldaña-

Vázquez & Munguía-Rosas, 2013; Perks & Goodenough, 2020). While previous research has

shown that some aerial insectivorous bat species respond to moonlight in undisturbed tropical

97 rainforest (Appel *et al.*, 2017, 2019), such effects have rarely been evaluated in the context of

98 human-modified landscapes (Jung & Kalko, 2011; Lima & O'Keefe, 2013; Kolkert *et al.*,

99 2020 but see Musila *et al.*, 2019). Assessing the effect of moonlight on the activity patterns of

100 aerial insectivorous bats in human-modified landscapes is important to understand possible

101 changes in ecosystem services provided by this bat ensemble (Pianka, 1973; Presley *et al.*,

102 2009). In agricultural landscapes, this issue is relevant for the management of fragments

103 because of the potential role of insectivorous bats in the suppression of agricultural pests

104 (Kemp *et al.*, 2019).

105   Here, we used the experimentally fragmented landscape of the Biological Dynamics

106 of Forest Fragments Project (BDFFP) in the Brazilian Amazon to evaluate the hypothesis that

107 moonlight modulates the effects of habitat disturbance on aerial insectivorous bat activity at

108 different temporal scales. We acoustically quantified bat activity in continuous forest and in

109 disturbed habitats (forest fragments and within the intervening secondary forest matrix) to

110 understand variation in species-level activity across these habitat types in relation to

111 moonlight. We conducted our analyses at different temporal resolutions, focussing on

112 variation in moonlight intensity: i) associated with the lunar cycle, ii) between dark and

113 bright nights, and iii) within nights. Accordingly, we predicted that:

114 i. Species sensitive to habitat disturbance and moonlight will respond negatively to

115   moonlight intensity in fragments and secondary forest, as previous research indicates

116   that some Amazonian aerial insectivorous bats respond to habitat disturbance (Núñez

117   *et al.*, 2019) and moonlight (Appel *et al.*, 2017).

118 ii. Species sensitive to habitat disturbance and moonlight will show increased activity in

119   fragments and secondary forests on dark nights (associated with new moon) compared

120   to bright nights (associated with full moon), whereas in continuous forest responses to

121   moonlight will be species-specific.

122   iii. In fragments and secondary forest, bat species will reduce activity in the early evening

123   to avoid the time of greatest predation risk. In continuous forest, within-night activity

124   will be concentrated in the early evening, both on bright and dark nights, to maximize

125   foraging opportunities during the peak in prey abundance.

126

127 **Material and Methods**

128 **Study site**

129   The study was conducted at the Biological Dynamics of Forest Fragments Project

130 (BDFFP) (2°25'S; 59°50'W), located ~80 km north of Manaus, Brazil (Fig. 1), a long-term

131 fragmentation experiment that has been running for ~40 years to study the effects of forest

132 fragmentation on Amazonian biota (Laurance *et al.*, 2018). The climate is characterized by a

133 dry season from July to November when precipitation drops below 100 mm/month and a

134 rainy season from November to June, when precipitation can exceed 300 mm/month (Ferreira

135 *et al.*, 2017). The study landscape consists of 11 forest fragments (five of 1 ha, four of 10 ha

136 and two of 100 ha), surrounded at the time of the study by a matrix of tall secondary forest,

137 and extensive areas of continuous primary forest that act as experimental controls (Laurance

138 *et al.*, 2018). In the early 1980s, forest fragments were experimentally isolated and the

139 vegetation around them has since been periodically cleared to maintain isolation, last in 2014

140 (Rocha *et al.*, 2017a), after data collection for this study. The site supports lowland evergreen

141 *terra firme* rainforest at 50 to 100 m of elevation, and the temperature ranges from 19 to 39

142 °C (Laurance & Williamson, 2001). The secondary forest is dominated by *Vismia* spp. in

143 areas that were cleared and burned and dominated by *Cecropia* spp. in areas that were only

144 cleared (Mesquita *et al.*, 2001). Percent canopy cover varies little between habitat types (

145 continuous forest interiors: 85.4 ± 5.2 [mean ± *SD*], fragment interiors: 87.4 ± 1, secondary

146 forest: 75.1 ± 6.7; Rocha *et al.*, 2017a). Canopy height in the largest fragments and

147   continuous forest averages 28 m (Almeida *et al.*, 2019), while in the well-developed

148   secondary forest the average canopy height is 15 m (Jakovac *et al.*, 2014; Mokross *et al.*,

149   2018).

150

151   **Bat acoustic sampling**

152   We sampled 13 sites across the BDFFP landscape between 2011 and 2013: three in

153   continuous forest (Cabo Frio, Florestal and Km 41 camps), six forest fragments (3 fragments

154   of 1 and 10 ha in Colosso, Dimona and Porto Alegre camps) and four in the secondary forest

155   matrix (Cabo Frio, Colosso, Dimona, Florestal and Porto Alegre camps) (Fig. 1). Each site

156   was visited twice during both dry and rainy seasons. At each sampling site, we installed an

157   automatic ultrasound recorder (Song Meter SM2Bat+) with an omnidirectional ultrasonic

158   SMX-US microphone (Wildlife Acoustics, Inc., USA) placed at a height of 1.5 m above the

159   ground (López-Baucells *et al.*, 2019). Ultrasound recorders were positioned in the center of

160   the fragments, in the secondary forest 100 m away from the edge of each fragment, and in the

161   interior of continuous forest 1000 m away from the edge. The recorders were configured to

162   passively register bat activity in real time, with a full spectrum resolution of 16 bit, a high-

163   pass filter set at fs/32 (12 kHz), and an adaptive trigger level relative to noise floor of 18

164   SNR. The SM2Bat units were programmed to record bat activity between 18:00 and 06:00

165   for four to five consecutive nights per sampling site (Table S1). Total sampling effort was

166   727 nights, with 8,278 recording hours. The number of sampling nights in each season was

167   similar in fragments and secondary forest (Table S1). Although for continuous forest

168   sampling effort was higher in the dry season (Table S1), we contend that the number of

169   nights sampled in the rainy season (77 nights) was sufficient to avoid seasonal biases, and

170   differences in sampling effort were also accommodated in the analysis.

171   All recordings were split into five-second segments and a bat pass was defined as a

172   sequence with a minimum of two recognizable search phase calls per species in each five-

173   second segment (Torrent *et al.*, 2018; Appel *et al.*, 2019). All bat passes were manually

174   identified to species or sonotype level following López-Baucells *et al.* (2016). We used

175   Kaleidoscope Pro Software (version 4.0.4.) (Wildlife Acoustics, Inc. Maynard,

176   Massachusetts, USA) for manual verification. Activity was calculated as the sum of five-

177   second segments with bat passes per night (nightly activity) and per hour (hourly activity).

178   In the total of ~190,000 bat passes we identified 18 aerial insectivorous bat species

179   and four sonotypes. We minimized potential detection biases by focusing on species that

180   were detected in at least 10% (73 nights) of the total nights and in all three sampling years.

181   This resulted in the selection of nine species for analysis: *Pteronotus alitonus*, *P. rubiginosus*

182   (revised by López-Baucells *et al.*, 2018; Pavan, Bobrowiec & Percequillo, 2018), *Furipterus*

183   *horrens*, *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura*,

184   *Myotis riparius* and *Eptesicus brasiliensis* (Table S2).

185

186   **Moonlight intensity**

187   Moonlight intensity for each night was estimated using the "sunmoon" software

188   (Conrad, 2017), a robust method for quantifying the amount of sunlight reflected by the

189   moon. This software employs the illuminance model of Janiczek & DeYoung (1987). To test

190   whether bat activity varied between dark and bright nights, we classified those nights with 0–

191   30% moon illuminated as dark and those with 70–100% as bright, following Appel *et al.*

192   (2017, 2019). We used this broad categorization instead of the moon phase because

193   moonlight intensity can vary greatly within the same moon phase (e.g. moonlight intensity in

194   the waning phase can vary from 3% to 55%, Appel *et al.*, 2017). Indeed, we used this

195   categorization because these nights are characterized by little variation in moon presence

196   (during bright nights) and absence (during dark nights) in order to avoid the influence of

197   moonrise and moonset times on bat activity (Appel *et al.*, 2017).

198   Cloud presence can influence the amount of moonlight that penetrates the forest, and

199   thus potentially distort bat activity responses to moonlight. In order to test for an effect of

200   cloud presence, we used data on cumulative rainfall per hour collected at the metereological

201   tower of the Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA) ZF-3

202   installed at KM 34 within the BDFFP. Nights were considered "cloudy" when rainfall ranged

203   from 0.1 to 10 mm/h, generally classified as weak to moderate rain (Appel *et al.*, 2019;

204   Vásquez *et al.*, 2020). Nights with more than 10 mm rain per hour were nights with heavy

205   rain, therefore were removed from the analyses (Carvalho *et al.*, 2011).

206

207   **Data analysis**

208   To model the effects of habitat type (continuous forest, fragments and secondary

209   forest) and moonlight on species-specific bat activity levels, we performed generalized linear

210   mixed models (GLMMs) using the function glmmTMB from the package "glmmTMB"

211   (Bolker *et al.*, 2020). The response variable in the GLMM models was the number of bat

212   passes recorded in a single night per species. Models were fitted using a negative binomial

213   distribution and, whenever the respective activity distribution showed a signal of zero

214   inflation, were implemented as zero-inflated models (Zuur *et al.*, 2008). For each model,

215   habitat type was specified as categorical fixed effect and moonlight as a continuous fixed

216   effect (percentage of moonlight intensity) and sampling night nested within research camp as

217   a random effect. We chose to model moonlight intensity only jointly with habitat type

218   because we were interested in evaluating the effect of moonlight for each habitat and not its

219   independent effect. The aforementioned random effects structure was chosen to account for

220   not only the spatial but also the temporal autocorrelation of the data - moonlight intensity of

221   one night depends on the moonlight intensity of the previous night. To compensate for

222   differences in sampling effort between habitat types (Table S2), we used the log-transformed

223   sampling effort per habitat type as offset in all models. Parameter estimates were visualized

224   using R package "ggstatsplot" (Patil, 2020). We used the full data set of the 727 sampling

225   nights in the GLMMs. To test if cloud presence affects bat activity, we performed GLMMs

226   analyzing bat activity in relation to moonlight, cloud presence and their interaction effect.

227   There was no effect of cloud presence on the activity of any of the focal bat species (Table

228   S3).

229   For each habitat type, differences in bat activity levels between dark and bright nights

230   were visualized using Gardner-Altman estimation plots and statistically evaluated using non-

231   parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95%

232   confidence intervals for the difference of means using R package "dabestr". Statistical

233   significance of the difference between dark and bright nights was determined based on the

234   lack of overlap in the frequency distributions of the data sets (Ho *et al.*, 2019).

235   Hourly activity levels between dark and bright nights for each habitat type were

236   compared using Kolmogorov-Smirnov 2-sample tests. Bat activity was pooled into 12

237   sampling intervals (hourly intervals) - e.g. bat passes recorded between 18:00 and 18:59 were

238   assigned to the same time interval (18:00). For comparisons between dark and bright nights,

239   we used data from 206 nights in continuous forest (118 dark, 88 bright), 124 nights in

240   fragments (65 dark, 59 bright) and 195 nights in secondary forest (97 dark, 98 bright). All

241   analyses were conducted in softwares R 4.0.2 and R Studio 4.0.2 (R Core Team, 2020;

242   RStudio Team, 2020).

243

244   **Results**

245   **Bat activity responses to habitat type**

246   Based on the GLMM results, habitat type had by far the greatest effect on bat activity.

247   Most significant responses were observed for secondary forest, followed by fragments (Fig.

248   2). Six species (*S. bilineata, S. leptura*, *C. maximiliani*, *C. brevirostris*, *E. brasiliensis* and *F.*

249   *horrens*) exhibited reduced activity in secondary forest, whereas *P. alitonus* and *P.*

250   *rubiginosus* showed elevated activity levels in this habitat (Fig. 2). On the other hand, two

251   species (*P. alitonus* and *F. horrens*) had significantly lower activity in fragments than in

252   continuous forest (Fig. 2).

253

254   **Bat activity responses to habitat type and moonlight intensity**

255   The activity of three species (*P. rubiginosus*, *S. bilineata* and *E. brasiliensis*) in

256   fragments was negatively affected by moonlight as suggested by the significant interaction

257   effect (Fig. 2). Similarly, moonlight significantly curtailed activity levels of *P. alitonus* and

258   *P. rubiginosus* in secondary forest, albeit the effect was small (Fig. 2).

259   In relation to habitat-specific comparisons of activity between dark and bright nights,

260   all species, except *S. leptura,* showed changes in activity between dark and bright nights in

261   some habitat type (Fig. 3). In continuous forest, *P. rubiginosus* and *P. alitonus* were more

262   active on bright nights, whereas *F. horrens* had greater activity during dark nights (Fig. 3).

263   *Pteronotus rubiginosus, S. bilineata, C. maximiliani, C. brevirostris, M. riparius* and *E.*

264   *brasiliensis* exhibited greater activity during dark than bright nights in fragments (Fig. 3). In

265   secondary forest, only *P. alitonus* and *P. rubiginosus* showed greater activity on dark nights,

266   opposite to the pattern in continuous forest (Fig. 3).

267   Hourly activity varied little between dark and bright nights and only five species

268   exhibited some change in activity pattern between dark and bright nights in the same habitat

269   (Table 2; Fig. S1). In continuous forest, *P. rubiginosus* and *S. leptura* were more active on

270   bright nights. On the other hand, hourly activity of *C. maximiliani* and *F. horrens* steadily

271   decreased on bright nights in continuous forest. In these two species, activity on dark nights

272   increased at the end of the night. In fragments, *M. riparius*, *P. rubiginosus* and *C.*

273   *maximiliani* increased their activity on dark nights, with greater activity in the middle of the

274   night in the latter two species. In secondary forest, only *P. rubiginosus* showed significant

275   differences, with an elevated activity during dark nights.

276

277   **Discussion**

278   Numerous studies have targeted the effects of forest fragmentation on tropical bats

279   (Meyer, Struebig & Willig, 2016; Mendes & Srbek-Araujo, 2020). Yet, in the Neotropics,

280   most research has been limited to the impacts of fragmentation on phyllostomid bats (e.g.

281   Klingbeil & Willig, 2009; Rocha *et al.*, 2017b, 2018), and fragmentation effects on aerial

282   insectivores remain poorly explored (but see Estrada-Villegas, Meyer & Kalko, 2010; Núñez

283   *et al.*, 2019). Over the past two decades, intensive research at the BDFFP has provided

284   valuable information about taxonomic, functional, phylogenetic and behavioural responses of

285   bats to the dynamic nature of fragmented landscapes (e.g. Bobrowiec & Gribel, 2010;

286   Farneda *et al.*, 2015; Rocha *et al.*, 2018, 2020; Aninta *et al.*, 2019). Although less researched

287   than their phyllostomid counterparts, aerial insectivorous bats at the BDFFP were found to

288   exhibit trait-related responses to fragmentation, with understory and constant-frequency and

289   frequency-modulated echolocating bats being particularly vulnerable to forest disturbance

290   (Núñez *et al.*, 2019). Here, we further advance current understanding about the responses of

291   aerial insectivorous bats to fragmentation, by analyzing how temporal activity patterns of this

292   bat ensemble are molded by variation in moonlight intensity. As hypothesized, we found that

293   moonlight can modulate responses to habitat disturbance but only in extremely bright nights.

294   Importantly, a joint effect of moonlight and habitat disturbance was most evident only in

295   species that emit constant-frequency calls (*Pteronotus* spp.).

296   Our results show that Amazonian aerial insectivorous bats respond more to habitat

297 type than to the interaction between habitat and moonlight. Most species had lower activity in

298 secondary forest and two showed lower activity in fragments compared to continuous forest.

299 This suggests that despite ca. 30 years of secondary forest regeneration, secondary forest is

300 still less attractive as foraging habitat for most aerial insectivorous bat species. These results

301 are consistent with those commonly reported for gleaning animalivorous bats, whose capture

302 rates typically decrease in disturbed habitats (Rocha *et al.*, 2017b; Webala *et al.*, 2019; Willig

303 *et al.*, 2019), probably due to being poorer foraging and roosting areas (Meyer & Kalko,

304 2008; Carballo-Morales, Saldaña-Vásquez & Villalobos, 2021). Yet, they contrast with

305 results from nectarivorous and frugivorous bats, which normally increase in abundance in

306 fragments and in secondary forest due the higher density of food resources (Bobrowiec &

307 Gribel, 2010; Farneda *et al.*, 2015).

308   The effect of moonlight intensity on activity differed between habitat types for *P.*

309 *alitonus*, *P. rubiginosus*, *S. bilineata* and *E. brasiliensis*. These four species exhibit a flexible

310 behaviour, changing their activity in disturbed environments when light conditions are not

311 favourable. The interaction between fragmentation and moonlight shows that for some

312 species the effects of fragmentation can be more acute than expected, since at least during

313 part of the lunar cycle their activity in fragments may be suppressed.

314   Bat activity over the lunar cycle is shaped by predator-prey interactions, as aerial

315 insectivorous bats are simultaneously predators and prey (Lang *et al.*, 2006; Vásquez, Grez &

316 Pedro, 2020). *Pteronotus rubiginosus* and *P. alitonus* increase their activity with moonlight in

317 continuous forest probably due to higher foraging success, as some insect orders increase

318 their activity in nights of high moon illumination (Kolkert *et al.*, 2020). The observed lunar

319 philia of *P. rubiginosus* agrees with the pattern found in other areas of Amazonian continuous

320 forest (Appel *et al.*, 2017; Durán & Oviedo Morales, 2019). On the other hand, the observed

decrease in the activity of *Pteronotus* spp. with increasing moonlight indicates that in disturbed areas the perceived risk of predation is probably greater. These bats may avoid leaving fragments as some visually oriented avian predators forage preferentially along fragment edges and open areas (Chalfoun, Thompson & Ratnaswamy, 2002; Spanhove *et al.*, 2009).

Although the interactive effect of moonlight and habitat type on bat activity was weak, our analyses showed that the effects of habitat type were most evident when evaluated at the extremes of the lunar cycle (dark *vs.* bright nights). In fragments, the activity of six species decreased on very bright nights, whereas, with the exception of *P. alitonus* and *P. rubiginosus* (which showed greater activity on bright nights in continuous forest), it was unaltered in continuous forest. The home ranges of aerial insectivorous bats (e.g. *P. parnelli* and *S. bilineata*) are generally much greater than the size of fragments studied (≤10 ha; Bradbury & Vehrencamp, 1976; Estrada, Coates-Estrada, & Meritt, 1993; Hoffmann *et al.*, 2007). As such, bats inhabiting forest fragments might need to forage/commute in the surrounding matrix, which on brighter nights, may increase exposure to predators. This increase in predation risk may therefore reduce bat activity in small fragments during nights with more intense moonlight (Bowers & Dooley, 1993). Thus, on bright nights probably bats reduced their home range avoiding the edges of the fragments, specially *Pteronotus* spp., since they are less active in secondary forest on bright nights.

The two extremes of the lunar cycle, bright *vs.* dark nights, had little effect on hourly activity levels indicating that bats do not respond to changes in moonlight during short periods of time. Yet, two species had higher hourly activity on bright nights in continuous forest and two species were more active at the end of dark nights. However, in fragments, hourly activity only changed for three species, all exhibiting lower activity at dusk on bright nights, which might be a strategy to reduce predation risks (Appel *et al.*, 2017). A similar

346 result was found for phyllostomids in early successional forest, small agricultural fields and

347 forest subjected to reduced-impact logging in the Amazon (Castro-Arellano *et al.*, 2009;

348 Presley *et al.*, 2009). *Cormura brevirostris* and *S. bilineata* did not change the hourly activity

349 between the extremes of brightness. This may relate with their foraging strategies (Gomes,

350 Appel & Barber, 2020), as both species have been suggested to feed closer to vegetation in

351 brighter nights (Jung & Kalko, 2010). The apparent absence of a moon effect on hourly

352 activity of insectivorous bats was also found by Appel *et al.*, (2017) in a continuous forest

353 location in Central Amazonia and by Thomas & Jacobs (2013) in South Africa.

354   Our results show that moonlight is an abiotic variable that can modulate bat activity

355 levels in tropical human-altered landscapes, but for most aerial insectivorous species the

356 effect is either weak or absent, and responses are more evident only in extremely bright

357 nights in fragments. Species that emit constant frequency calls such as *P. rubiginosus* and *P.*

358 *alitonus* showed the strongest response in activity levels as manifested by a change from a

359 positive relationship with moonlight in continuous forest to a negative one in fragments and

360 secondary forest. Therefore, moonlight can augment the effects of fragmentation on the

361 activity of bats that echolocate using constant frequency calls. This is concerning because

362 habitat disturbance might reduce the temporal window in which foraging conditions are

363 favorable and thus limit the ability of species to meet their daily dietary requirements

364 (Vásquez, 1994; Castro-Arellano *et al.*, 2009; Rocha *et al.*, 2020). This physiological stress

365 may increase exposition to pathogens (Turmelle & Olival, 2009), and there are several

366 examples of how anthropogenic land-use change can have a major impact on the infection

367 and circulation of zoonoses (Gibb *et al.*, 2020; White & Razgour, 2020). Future research

368 investigating how behavioral responses translate into fitness consequences (e.g. mortality and

369 reproductive success) in fragmented landscapes is needed to better understand long-term

370 population persistence.

Conservation implications

Fragmentation and forest disturbance have been identified as the major causes of
biodiversity loss in the tropics. Some of the insectivorous bat species studied here are
fragmentation sensitive (Núñez *et al.* 2019). In our study, habitat disturbance was the main
factor underlying decreases in the activity of aerial insectivorous bats, but moonlight
accentuated reductions in activity for some species in fragments and might impact their
capacity to provide their crucial ecosystem services as insect predators. Insectivorous bats are
key suppressors of herbivorous insects in both humanized and natural habitats and they can
prevent rice loss at an estimated cost of $1,2 million/year and more than $3,7 billion/year in
general agricultural losses (Boyles *et al.*, 2011; Wanger *et al.*, 2014; Kemp *et al.*, 2019).
However, it is important to mention that the BDFFP fragments are surrounded by secondary
forest at an advanced stage of succession, which can buffer the impacts of fragmentation and
create better foraging conditions for aerial insectivorous bats than in other human-modified
landscapes (Rodríguez-San Pedro & Simonetti, 2015). Fragments in landscapes dominated by
large-scale agriculture commonly exhibit abrupt margins, are embedded within a
homogeneous matrix and suffer additional anthropogenic disturbances (e.g., effects of roads
and artificial illumination) which may considerably reduce the ecological services provided
by light-sensitive bat species (Put, Fahrig & Mitchell, 2019).

Artificial light at night has been increasing over time in biodiversity hotspots (Guetté
et al., 2018) and this is concerning because the increasing human pressure in the periphery of
forested areas can leave forest fragments in a state of constant illumination during the night.
Although artificial light attracts insects consumed by insectivorous bats, some bat species
studied here are sensitive to urbanization (Jung & Kalko, 2010; Alpízar, Rodríguez-Herrera,
& Jung, 2019). It is known that lit areas can influence the quality of roosts and fragment

16

commuting routes for some bat species with negative consequences for the reproduction and

behaviour of bats (Downs *et al.*, 2003; Laforge *et al.*, 2019; Straka *et al.*, 2019). In view of

the recent increase of fragmentation and artificial light at night in the Brazilian Amazon due

the development of cities, agricultural areas and expanding road networks (Haddad *et al.*,

2015; Lovejoy & Nobre, 2018; Vilela *et al.*, 2020), the protection of undisturbed forests is

crucial for the conservation of light-sensitive aerial insectivorous bats. Moreover, bats

actively prey on mosquitoes responsible for disease transmission (Puig-Montserrat *et al.*,

2020) and as tropical urban areas have a proliferation of these insects, the promotion of large

forest fragments in urban areas can be an alternative to attract more activity of insectivorous

bats.

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722

723   **Figure legends**

724   **Figure 1.** Location of the Biological Dynamics of Forest Fragments Project (BDFFP) and the

725   distribution of sampling points in continuous forest, fragments of 1 and 10 ha, and secondary

726   forest. Continuous forest is represented in dark gray and secondary forest (matrix) in light

727   gray. The map in the upper right corner shows the location of the study area in the Central

728   Amazon. The schematic figure illustrates the vegetation structure in the three habitat types.

729

730   **Figure 2.** Effects of moonlight, habitat type, and their interaction on activity of the nine focal

731   species in the BDFFP evaluated using generalized linear mixed models. Effect estimates are

732   based on the fixed effect posterior distribution, characterized by its mean (dot) and credible

733   intervals (95% CI, lines). Gray circle estimates indicate significant negative effects, white

734   circle estimates significant positive effects and black estimates non-significant effects.

735

736   **Figure 3.** Gardner-Altman estimation plots showing the effect size (mean difference) of bat

737   activity between dark and bright nights in each type of forest - continuous, fragments and

738   secondary forest at the BDFFP. Dark nights were considered those with between 0 and 30%

739   moonlight intensity and bright nights those above 70%. The mean is indicated by a dot, error

740   bars represent the 95% confidence interval. Gray circle estimates indicate significant negative

741   effects (higher activity on dark nights), white circle estimates significant positive effects

742   (higher activity on bright nights) and black estimates non-significant effects.

743

744   **Figure 4.** Hourly activity of nine species of aerial insectivorous bat in each habitat type

745   (continuous forest, fragments and secondary forest) on dark nights (0-30% of moonlight

746   intensity) and bright nights (70-100% of moonlight intensity). Black lines denote dark nights,

747   gray lines bright nights. The solid line is the average activity and the dotted line represents

748   the standard deviation of activity. * indicates a significant difference between dark and bright

749   nights based on Kolmogorov-Smirnov 2-sample tests.

750

751   **Supporting Information**

752   Additional supporting information may be found online in the Supporting Information section

753   at the end of the article.

754

755   **Table S1.** Number of hours recorded in each habitat type and each season sampled.

756   **Table S2.** Number of bat passes recorded for the nine aerial-insectivorous bat species

757   studied.

758   **Table S3.** Summary of GLMMs examining the influence of cloud presence, moonlight and

759   their interaction on bat activity.

760   **Table S4.** Number of bat passes in dark and bright nights for the nine aerial-insectivorous bat

761   species studied.

762   **Table S5.** Summary of GLMMs examining the influence of habitat type and the interaction

763   between moonlight and habitat type on bat activity.

764   **Table S6.** Results of Kolmogorov-Smirnov 2-sample tests comparing the hourly activity

765   between dark and bright nights in each habitat type sampled.