High moon brightness and low ambient temperatures affect sloth predation by harpy eagles

Everton B. P. de Miranda [Corresp., 1] , **Caio F. Kenup** [2] , **Edwin Campbell-Thompson** [3, 4] , **Felix H. Vargas** [4] , **Angel Muela** [4] , **Richard Watson** [4] , **Carlos A. Peres** [5, 6] , **Colleen T. Downs** [1]

[1] School of Life Sciences, Centre for Functional Biodiversity, University of KwaZulu-Natal, Pietermaritzburg, Pietermaritzburg, KwaZulu-Natal, South Africa

[2] Wildlife and Ecology Group, Massey University, Palmerston North, New Zealand

[3] Fundación Aguilas de Los Andes, Pereira, Colombia

[4] The Peregrine Fund, Boise, United States of America

[5] School of Environmental Sciences, University of East Anglia, Norwich, United Kingdom

[6] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

Corresponding Author: Everton B. P. de Miranda
Email address: mirandaebp@gmail.com

Background. Climate plays a key role in the life histories of tropical vertebrates. However, tropical forests are only weakly seasonal compared with temperate and boreal regions. For species with limited ability to control core body temperature, even mild climatic variation can determine major behavioural outcomes, such as foraging and predator avoidance. In tropical forests, sloths are the arboreal vertebrate attaining the greatest biomass density, but their capacity to regulate body temperature is limited, relying on behavioural adaptations to thermoregulate. Sloths are largely or strictly nocturnal, and depend on crypsis to avoid predation. The harpy eagle (*Harpia harpyja*) is a sloth-specialist and exerts strong top-down control over its prey species. Yet the role of environmental variables on the regulation of predator-prey interactions between sloths and harpy eagles are unknown.

Methods. Our study was conducted between 2003 and 2009 at Soberanía National Park (SNP), Panamá. The SNP has a marked dry season from December to April, and a wet season from May to November. Dry season mean temperatures were 27.3°C, and warmer than the wet season mean 26.5°C. The harpy eagle is considered Near Threatened. This motivated a comprehensive effort to reintroduce this species into parts of Mesoamerica. This effort incidentally enabled us to understand the prey profile of harpy eagles over multiple seasons. Telemetered harpy eagles were seen hunting and feeding on individual prey species. For each predation event, field assistants systematically recorded the species killed. We analysed the effects of climatic conditions and vegetation phenology on the prey species profile of harpy eagles using generalised linear mixed models.

Results. Here we show that sloth predation by harpy eagles was negatively affected by nocturnal ambient light (i.e. bright moonshine) and positively affected by seasonally cool temperatures. We suggest that the first ensured low detectability conditions for sloths foraging at night and the second posed a thermally unsuitable climate that forced sloths to forage under riskier daylight. We showed that even moderate seasonal variation in temperature can influence the relationship between a keystone tropical forest predator and a dominant prey item. So predator-prey ecology in the tropics can be modulated by subtle changes in environmental conditions. The seasonal effects shown here suggest important demographic consequences for sloths, which are under top-down regulation from harpy eagle predation, perhaps limiting their geographic distribution at higher latitudes.

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8 Everton B. P. Miranda[1], Caio Fittipaldi Kenup[2], Edwin Campbell-Thompson[3, 4], Félix Hernán

9 Vargas[4], Angel Muela[4], Richard Watson[4], Carlos A. Peres[5, 6], Colleen T. Downs[1]

11 [1] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal,

12 P/Bag X01. Pietermaritzburg, 3209, South Africa

13 [2] Wildlife and Ecology Group, Massey University, Palmerston North, New Zealand

14 [3] Fundación Águilas de Los Andes, Pereira, Colombia

15 [4] The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, Idaho 83709 U.S.A

16 [5] School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK

17 [6] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

18 Corresponding Author:
19 Everton Miranda
20 Rua F2, nº220, Alta Floreta, Mato Grosso 78580-000, Brazil
21 Email address: mirandaebp@gmail.com

23 Running header: Sloth predation by harpy eagles
24

Abstract

Background. Climate plays a key role in the life histories of tropical vertebrates. However, tropical forests are only weakly seasonal compared with temperate and boreal regions. For species with limited ability to control core body temperature, even mild climatic variation can determine major behavioural outcomes, such as foraging and predator avoidance. In tropical forests, sloths are the arboreal vertebrate attaining the greatest biomass density, but their capacity to regulate body temperature is limited, relying on behavioural adaptations to thermoregulate. Sloths are largely or strictly nocturnal, and depend on crypsis to avoid predation. The harpy eagle (*Harpia harpyja*) is a sloth-specialist and exerts strong top-down control over its prey species. Yet the role of environmental variables on the regulation of predator-prey interactions between sloths and harpy eagles are unknown.

Methods. Our study was conducted between 2003 and 2009 at Soberanía National Park (SNP), Panamá. The SNP has a marked dry season from December to April, and a wet season from May to November. Dry season mean temperatures were 27.3°C, and warmer than the wet season mean 26.5°C. The harpy eagle is considered Near Threatened. This motivated a comprehensive effort to reintroduce this species into parts of Mesoamerica. This effort incidentally enabled us to understand the prey profile of harpy eagles over multiple seasons. Telemetered harpy eagles were seen hunting and feeding on individual prey species. For each predation event, field assistants systematically recorded the species killed. We analysed the effects of climatic conditions and vegetation phenology on the prey species profile of harpy eagles using generalised linear mixed models.

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53   in the tropics can be modulated by subtle changes in environmental conditions. The seasonal

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55   down regulation from harpy eagle predation, perhaps limiting their geographic distribution at

56   higher latitudes.

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Introduction

59

60 Predation is a central theme in ecology and evolution, driving morphological, physiological, and

61 behavioural responses in prey species to the threat of death or injury (Genovart et al., 2010).

62 Both the nature and magnitude of predation as a dominant ecological force are affected by

63 seasonality (Darimont & Reimchen, 2002). However, the seasonality of predator-prey

64 relationships in tropical forests is at best considered to be subtle compared with temperate and

65 boreal regions, because of the comparatively low variation in day length and ambient

66 temperature (Forsythe et al., 1995). Nevertheless, tropical forests can experience considerable

67 seasonality in leaf flushing and fruiting as a response to climatic variables (Mendoza, Peres &

68 Morellato, 2016). While available data suggests that climatic conditions in tropical environments

69 have strong effects on animal activity (Foster et al., 2013; Cid, Oliveira-Santos & Mourão,

70 2015), there are relatively few studies about the nature of such effects on predator-prey

71 interactions.

72   Seasonally elevated rainfall and the resulting responses in vegetation growth can provide

73 food and cover for many arboreal taxa in tropical forests (Haugaasen & Peres, 2009).

74 Conversely, the dry season often induces leaf abscission in trees and woody lianas (Souza,

75 Gandolfi & Rodrigues, 2014), which may limit food availability and shelter to arboreal folivores.

76 The combination of reduced cover and limited food resource availability can enhance predation

77 risk (Menezes, Kotler & Mourão, 2014; Menezes, Mourão & Kotler, 2017). The seasonal

78 variation may modify the range of thermal microhabitats available to a prey species. As

79 endothermic forest specialists, sloths (genus *Bradypus* and *Choloepus*, order Pilosa) exhibit

80 relatively low basal metabolic rates and can only partially regulate body temperature (Pauli et al.,

81 2016). Therefore, they need to bask and can be affected by even mild variation in habitat cover

82 and thermally inappropriate microhabitats (Peery & Pauli, 2014; Giné et al., 2015), to the extent

83 that temperature seasonality is highly influential on sloth behavioural ecology (Moreira et al.,

84 2014).

85   Sloths from the *Bradypus* and *Choloepus* genus differ in their biology. *Choloepus* are

86 more vigorous (Pauli et al., 2016), larger (~6kg, Wetzel & Montgomery, 1985), have a higher

87 body temperature (Vendl et al., 2016), and a more diversified diet (Dill-McFarland et al., 2016).

88 *Bradypus* sloths fit the stereotypical sluggish behaviour of sloths (Pauli et al., 2016), are smaller

89 (~4kg; Wetzel & Montgomery, 1985), have a relatively low body temperature (Vendl et al.,

90 2016), and feed on leaves exclusively (Dill-McFarland et al., 2016). Finally, two-toed sloths

91 (*Choloepus* spp.) are nocturnal, whereas three-toed sloths (*Bradypus* spp.) are cathemeral

92 (Sunquist & Montgomery, 1973; Giné et al., 2015).

93 Likewise, moonlight is likely to alter animal behaviour by affecting detectability of both

94 predators and prey at night (San-Jose et al., 2019). Lunar phobia by mammals is widely justified

95 as a strategy to prevent predation (Cozzi et al., 2012). However, a metanalysis by Prugh and

96 Golden (2014) showed that the response to lunar light was typically idiosyncratic. While

97 visually-oriented mammals have an increased activity response to lunar light, mammals that have

98 weak vision—like sloths—generally decrease activity on bright nights (Prugh & Golden, 2014)

99 and therefore are less likely to suffer predation.

100   We can expected that the seasonality of predator-prey relationships involving sloths

101 might be affected by even subtle climatic fluctuations in ambient temperature. Sloths are

102 important prey species that rely heavily on crypsis to avoid predation, rather than evasive

103 responses once they are detected (Touchton, Hsu & Palleroni, 2002). However, studies

104 attempting to identify the cues leading to seasonal changes in prey activity and predation are

105 inherently hindered by small sample sizes. While apex predators have profound effects on

106   ecosystem structure and function (Terborgh et al., 2001), they are difficult to study, rendering

107   this lack of knowledge almost impossible to overcome.

108   Harpy eagles (*Harpia harpyja*; Fig 1) are an apex predator that specialises on sloths,

109   relying heavily on these prey species wherever they co-occur (Aguiar-Silva, Sanaiotti & Luz,

110   2014; Miranda, 2015). Harpy eagles hunt passively by visually scanning and listening to the

111   forest canopy (Touchton, Hsu & Palleroni, 2002). They are unique among eagles having a large

112   retractable facial disc to enhance their hearing (Ferguson-Lees & Christie, 2001). Harpy eagles

113   are the Earth's largest eagles. Being large-sized, they can prey on sloths of any age (Aguiar-

114   Silva, Sanaiotti & Luz, 2014), including adult individuals of all continental sloth species

115   (Miranda, 2018). Harpy eagle-sloth predator-prey systems are therefore ideal candidates to

116   investigate how changes in climate and moonlight may affect multispecies predation rates.

117   The harpy eagle is considered Near Threatened by the IUCN (Birdlife International, 2017),

118   mainly because of human persecution (Muñiz-López, 2017) and habitat loss, which have

119   extirpated these mega-raptors from 41% of their former historical range distribution (Miranda et

120   al., 2019). This motivated The Peregrine Fund to lead a comprehensive effort to reintroduce this

121   species into parts of Mesoamerica (Campbell-Thompson et al., 2012; Watson et al., 2016). This

122   effort, spanning from 2003 to 2009, incidentally enabled us to understand, for the first time, the

123   prey profile of harpy eagles over multiple seasons.

124   We explored environmental determinants of prey capture rates of reintroduced harpy

125   eagles in Soberanía National Park; a tropical protected area in Panamá. Our goals were twofold:

126   (1) to assess the effects of seasonality—like temperature, rainfall and leaf decidousness—on

127   sloth capture rates by harpy eagles; and (2) to assess how moonlight could affect sloth and

128   nocturnal prey predation rates. We predicted that: (1) sloth predation rates would increase with

129 low temperatures, high rainfall and low leaf cover; (2) sloth and nocturnal prey predation rates

130 would increase with low moon brightness.

131

Materials & Methods

133 STUDY SITE. — Our study was conducted between 2003 and 2009 at Soberanía National Park

134 (hereafter, SNP), a 19,545 ha protected area in eastern Panama along the banks of the Panama

135 Canal (9°07'13" N, 79°39'37" W). The vegetation of SNP consists of semi-deciduous,

136 seasonally moist tropical forest, most of which is now advanced (>80 years) secondary forest

137 (Bohlman, 2010). The area has most of the staple prey species targeted by harpy eagles (Aguiar-

138 Silva, Sanaiotti & Luz, 2014), including three-toed sloths (*Bradypus variegatus*), Hoffman's

139 two-toed sloths (*Choloepus hoffmanni*), white-nosed coati (*Nasua narica*), northern lesser

140 anteater (*Tamandua mexicana*) and mantled howler monkeys (*Alouatta palliata*), all of which are

141 either strictly arboreal or scansorial mammals. The Peregrine Fund had conducted experimental

142 harpy eagle releases within SNP since 1997 (Muela et al., 2003; Watson et al., 2016), therefore

143 we assumed that none of the prey species here were predator-naïve during our study.

144   The SNP has a marked dry season from December to April and a wet season from May to

145 November. The wet season concentrates 85.3% of the annual rainfall, which averaged 2,242 mm

146 p.a. for 2003-2009. During the dry season, the mean, minimum and maximum ambient

147 temperatures were 27.3, 22.1, 33.0°C, respectively, and slightly warmer than the corresponding

148 temperatures during the wet season (26.5, 23.2, 30.9°C, respectively). Daily climate data were

149 obtained from ETESA (http://www.hidromet.com.pa/), using Hodges Hill Meteorological Station

150 data for rainfall (15 km from the release site) and the Tocumen Station for data on temperature

151 (43 km from the release site). A Walter-Lieth climate diagram describing the seasonality of

152 rainfall and ambient temperature in the park was created (Supplementary Information Fig. S1).

153   HARPY EAGLE PREY PROFILE.—Before final release, captive-bred harpy eagles were soft-

154 released at SNP by a process known as hacking (Muela et al., 2003). This allowed harpy eagles

155 to learn how to hunt, as would occur in the wild (Muñiz-López et al., 2016). Further details on

156 the harpy eagle reintroduction protocols and results are available in Campbell-Thompson et al.

157 (2012) and Watson et al. (2016). Harpy eagles were fitted with both radio-telemetry and GPS

158 tags. During soft releases, they were fed thawed rats and rabbits, always using a blind to avoid

159 food conditioning with humans. Foraging independence was defined on the basis on an eagle

160 being able to make two unassisted successive kills within 20 days or survive 30 days without

161 food provisioning, thereby demonstrating that it was able to hunt self-sufficiently. Both regular

162 radio- and global position system (GPS)-tracking leading to visual contact with each telemetered

163 eagle was required to check its body condition.

164   As the reintroduced hapy eagles were captive-born sub-adults (5-22 months; Campbell-

165 Thompson et al., 2012) from captive stock maintained by The Peregrine Fund, we performed an

166 *a priori* graphical analysis to ensure that the diet of reintroduced harpy eagles was similar to that

167 of wild adult individuals. We did so by dividing the number of captured prey items within blocks

168 of 25 samples (which adequately represents the main prey species; Miranda 2015) and

169 distributed them according to ontogeny or experience. We defined ontogeny as age in months for

170 any given predation event, whereas we defined experience as any given predation event relative

171 to the number of days since the first wild prey item was captured. Neither ontogeny nor

172 experience affected harpy eagles' patterns of predation as there was no evidence of nested

173 patterns that would be expected if shifts in prey preferences occurred (Supplementary

174   information Fig. S2 and S3). We therefore consider hunting patterns by reintroduced harpy

175   eagles comparable with those of wild adults, and this was consistent with previous reports

176   (Touchton, Hsu & Palleroni, 2002). The spatial distribution of those kill sites, as well as the

177   location of the release site and meteorological stations within SNP are shown in Fig. 2.

178   PREDATION AND ENVIRONMENTAL DETERMINANTS.— During observations, while tracking,

179   harpy eagles were seen hunting and feeding on individual prey species. For each predation event,

180   field assistants systematically recorded all species killed (whenever identification to the level of

181   species was possible). Field assistants were instructed to remain as inconspicuous as possible

182   and leave the eagles alone as soon as observations were recorded. Prey items of known species

183   identity were recorded during all months of the year, over the 7-year study, although

184   observations were typically sparser during the month of November.

185   We related measures of climatic seasonality and vegetation phenology to the prey species

186   profile of harpy eagles. Daily climatic data on precipitation and ambient temperature, were

187   obtained from nearby meteorological stations. Data on the phases of the lunar cycle at a daily

188   resolution over the entire study period were obtained from http://www.astronomyknowhow.com.

189   We used the percentage of moon shade cover per night as a proxy for light availability. We used

190   the snormalised difference vegetation index (NDVI) as a proxy for canopy leaf deciduousness,

191   where NDVI = (IR − R)/(R + IR), IR being the near- infrared LANDSAT band 4 and R the red

192   LANDSAT band 3. NDVI values were calculated using georeferenced LANDSAT images obtained

193   for all months of the year during the study period. NDVI is a measure of vegetation 'greenness',

194   rather than deciduousness, but is highly correlated to leafing cycles (Bohlman, 2010). For each

195   prey detection event, we estimated the NDVI score of all 30 m x 30 m pixels within a 1 km

196   radius of the location of each predation event for the nearest five dates of LANDSAT images

197   available for that period. We then interpolated these indices to estimate the composite NDVI

198   metric for the detection date of each prey item.

199   We ran two batches of sgeneralised linear mixed-effects models (GLMM) using as

200   response variables (1) the probability of any given prey item being a sloth (either *Bradypus* or

201   *Choloepus*) and (2) the probability of any given prey item being nocturnal. Because the set of

202   environmental covariates for each model was large, we used a backwards AIC-based stepwise

203   algorithm to select the most important variables for each fixed-effect model, adding the random

204   effect afterwards. All GLMMs were run using a binomial error structure and the logit link

205   function, and bird identity as a random effect on the intercept. All variables used were checked

206   for covariance using the Variance Inflation Factor (VIF). All analyses were run using the R 3.6.1

207   platform. Environmental covariates used in each GLMM are presented in Supplementary

208   information Table S1. All source codes used in the analyses are available at

209   https://github.com/KenupCF/HarpySlothPredation.

210   The Peregrine Fund Harpy Eagle Restoration Program complied with the laws of Panamá

211   during the time in which the project was performed, with permits granted by National

212   Environmental Authority of Panama (ANAM, at present MiAmbiente and SISBIO#58533-5).

213

Results

215   We recorded a total of 200 harpy eagle predation events, from which we obtained positional data

216   for 189 prey items, 173 of which were identified. These prey items were killed by 33 harpy

217   eagles during six dry seasons and six wet seasons during the 7 years of study. This amounted to

218   88 prey samples during the dry seasons and 85 samples during the wet seasons. The temporal

219   distribution of predation records and the functional groups of prey species showed that sloths

220   were by far the most important prey species for harpy eagles (Fig. 3). Two sloth species

221   represented 65.3% of the harpy eagle diet in terms of the overall numeric prey profile, of which

222   brown-throated sloths, Hoffman's two-toed sloths and unknown sloths represented 34.1%, 15.6%

223   and 15.6% of all prey items, respectively. Second to sloths, the next most significant dietary

224   contributors to harpy eagles were white-nosed coatis (7.5%), northern lesser anteaters (6.9%) and

225   mantled howler monkeys (5.2%). Further information on the prey species composition are shown

226   in Table 1.

227   Sloth predation rates increased significantly during low moon brightness ($\beta = -0.648$, p =

228   0.0116) and low ambient temperatures with marginal statistical significance ($\beta = -0.508$, p =

229   0.0535; Fig. 4). Harpy predation on nocturnal animals was weakly affected by low moon

230   brightness (Fig. 4), but this lacked sufficient statistical significance ($\beta = -0.392$, p = 0.1461).

231   Rainfall and leaf deciduousness had no discernible effect in any of our models. Statistical results

232   are summarised in Table 2.

233

234 **Discussion**

235 Although environmental conditions either increase prey vulnerability or provide an advantage to

236 sit-and-wait and pursuit predators (Doody, Sims & Letnic, 2007; Prugh & Golden, 2014), little

237 has been documented on this topic in closed-canopy tropical forest ecosystems. In harpy eagle-

238 sloth predator-prey systems, we showed increases in sloth nocturnal activity under elevated

239 moon brightness and cryptic behaviour during the day provided mechanisms of escaping

240 detection by harpy eagles. We also showed an increase in predation rates under cool

241 temperatures, which may induce further diurnal activity of sloths. Finally, we examined the roles

242 of leaf flush and rainfall on harpy eagle prey choice, but neither had a detectable effect on sloth

243 predation rates. These results pose interesting questions about the consequences of temperature

244 and moon brightness to this keystone Neotropical forest predator and its dominant prey species.

245   Moonlight has been shown to have contradictory effects on nocturnal mammal activity

246 patterns in terms of their antipredator strategies. Prey species that can detect predators visually

247 and anticipate their attacks with evasive manoeuvres may increase foraging activity under high

248 levels of moonlight, whereas those that cannot decrease activity (Prugh & Golden, 2014). Sloths,

249 however, typically prefer to sleep at night in environments where they evolved with predator

250 presence (Voirin et al., 2014), and in other areas generallyshowing greater fear of diurnal

251 predators as harpy eagles. Indeed, there is anecdotal evidence of increased sloth activity during

252 full moon phases (Beebe, 1926). Sloths are known to be lethargic and have extremely poor

253 vision, while harpy eagles typically attack from distances of less than 30 m during daylight

254 (Touchton, Hsu & Palleroni, 2002). We, therefore, expected that sloths reduce their overall

255 activity during the day, instead foraging at night under bright moonlit to reduce predation risk,

256 which significantly reduces the probability of successful attacks by diurnal harpy eagles. Success

257   rates of harpy eagles predation on sloths is generally high compared with visually oriented prey:

258   55% of all attacked sloths are successfully killed, while only 33% of visually oriented prey are

259   successfully killed if they had been attacked (Touchton, Hsu & Palleroni, 2002). This may be the

260   underlying adaptive reason why sloths are inactive during the day if bright nights are available as

261   foraging time, sneutralising search images of diurnal predators and greatly reducing their

262   detection probability by harpy eagles. Further sloth telemetry studies would provide

263   confirmatory evidence.

264   In addition to the reduced predation levels of sloths during bright moon nights, we

265   showed that as ambient temperatures increased, predation rates declined. Presumably, this

266   happened because of the increased daytime activity levels of this endotherm, which is prone to

267   metabolic torpor under cooler weather conditions, especially at night (Giné et al., 2015). It has

268   been shown, for instance, that the nocturnal activity of the maned sloth (*Bradypus torquatus*) is

269   inhibited by lower ambient temperatures (Chiarello, 1998). Predation rates of sloths by harpy

270   eagles were higher during colder conditions, which likely induce compensatory activity by sloths

271   during the warmer daytime. Basking behavior of sloths increases with lower ambient

272   temperatures along altitudinal gradients in mountainous areas (Urbani & Bosque, 2007). Another

273   possible explanation for the temporal changes in sloth predation rate could result from its

274   reproductive behaviour. However, the literature shows weak and idiosyncratic evidence for

275   seasonal breeding for both sloth species present in our study area (Taube et al., 2001). These

276   features reinforce our premise that behavioural crypsis is the main antipredator strategy of sloths,

277   which we suggest to be the underlying reasons for the patterns observed in our study. Indeed, the

278   latitudinal boundaries of the geographic distribution of sloths are far more restricted than those of

279   harpy eagles (Moreira et al., 2014; Miranda et al., 2019). Sloths of the *Choloepus* genus are

280 distributed over tropical Central America and the pan-Amazonian region, while *Bradypus* also

281 occur over the northern section of Atlantic Forest (Emmons & Feer, 1997). Predation by harpy

282 eagles may play a key role in limiting sloth geographic distribution—and altitudinal ranges—

283 given that sloths would be required to compensate for cooler temperatures in the southern

284 Atlantic Forest or higher regions by increasing levels of diurnal activity (Chiarello, 1998; Urbani

285 & Bosque, 2007). Therefore, this would inhibit extended periods of inactivity induced by cool

286 temperatures, but increase temporal activity overlap with diurnal predators.

287   Rainfall apparently had no effect in any of our models explaining the incidence of sloth

288 predation, a pattern that could also be explained by low predation risk resulting from the

289 cessation of harpy eagle activity during rainy weather (Touchton, Hsu & Palleroni, 2002), or

290 even distance from the meteorological stations, inducing error. Leaf abscission presented no

291 effects on predation of sloths. Although we spredicted increased probability of arboreal prey

292 detection under leafless conditions in the semi-deciduous forests of central Panama, forest areas

293 dominated by leafless trees and/or woody lianas may be consistently avoided by prey species

294 relying on concealed foraging activity (Menezes, Kotler & Mourão, 2014; Menezes, Mourão &

295 Kotler, 2017). For a sloth, leafless tree crowns offer little if any protective cover and no food

296 resources. Our robust methods to estimate levels of deciduousness combined with a wide buffer

297 describing the likely sight range of potential kills suggest that arboreal habitats lacking foliage

298 cover would be avoided not only by prey species but also by harpy eagles, thereby at least partly

299 explaining why deciduousness had no effects in any of our models.

300   Nocturnal prey capture by harpy eagles was not significantly affected by any of the

301 environmental covariates, and the fact that these large diurnal raptors can frequently successfully

302 kill several strictly nocturnal prey species remains puzzling. Modest increases in predation rates

303   of nocturnal mammals were associated with darker nights, when nocturnal species typically

304   preyed by harpy eagles (anteaters, opossums, and armadillos) are expected to be more active

305   given their poor ability to anticipate incoming predators visually (Caro, 2005; Prugh & Golden,

306   2014). The harpy eagle sit-and-wait predation strategy is further enhanced by their retractable

307   facial disc, which performs the same function as in strictly nocturnal raptors (i.e. owls), of

308   improving acoustic detection of prey. Combined with extremely acute vision, which is likely

309   associated with a high density of photoreceptor cells in the retina typical of many diurnal raptors

310   (Lisney et al., 2013), harpy eagles are superbly capable of locating inconspicuous prey, enabling

311   them to be the only Neotropical apex predator to specialise on the highly secretive sloths

312   (Miranda, 2015; Miranda, Menezes & Rheingantz, 2016). Harpy eagle activity patterns can be

313   investigated with further research using either intensive telemetry-assisted follows or camera

314   trapped nests. By including nocturnal telemetry or motion-sensitive telemetry devices on

315   monitoring schedules or confirming that harpy eagles can deploy crepuscular/nocturnal hunting

316   effort at the time of nesting (e.g. evidenced by nocturnal prey delivery) would largely solve this

317   question.

318   Our results suggest important consequences for patterns of prey mortality through the

319   tropical seasons of Neotropical forests. We, therefore, suggest that researchers, conservationists

320   and practitioners can learn from natural fluctuations in predator-prey systems when designing

321   management actions (such as reintroduction, release and translocation efforts) of both harpy

322   eagles and their prey, since some of these prey species are also threatened (Catzeflis et al., 2008;

323   Moreira et al., 2014; Suscke et al., 2016). For instance, consequences of the harpy eagle

324   reintroduction on the endemic maned sloth which is listed as Vulnerable in the Brazilian Atlantic

325   Forest needs careful evaluation.

326

Conclusions

328 We showed that the probability of harpy eagles preying on sloths decreased in response to

329 nocturnal high moon brightness and increased with low temperatures. This almost certainly

330 occurs because sloths respond to low temperatures foraging more in the daytime, and circumvent

331 high diurnal detectability by foraging on bright moonlit nights when they are not exposed to

332 visually oriented predators. These conceptually simple conclusions result from overcoming the

333 formidable challenges of monitoring the diet of apex predators in tropical forests for extended

334 periods. We further note that the seasonal effects we uncovered here suggest important

335 consequences for herbivore prey species, whose populations are likely regulated by top-down

336 predation from harpy eagles and other top predators. The magnitude of cyclic changes in

337 predator-prey interactions shown here potentially are even stronger in more seasonal tropical

338 and subtropical forests experiencing cooler seasons, higher altitudes or prolonged flood pulses.

339 Further studies on a diverse set of predator and prey assemblages in tropical forests elsewhere

340 would help fill this knowledge gap.

341

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354

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483

Figure 1

Fig. 1. Harpy eagle preying over sloth.

Adult female harpy eagle (*Harpia harpyja*) eating a young Two-toed sloth (*Choloepus didactylus*; Photo: Danilo Mota).

Figure 2

Fig. 2. Study site.

Location of Soberanía National Park in central Panama (lower left inset map), showing the location of 189 predation events (green dots), release site (white star) and meteorological stations (white triangles).

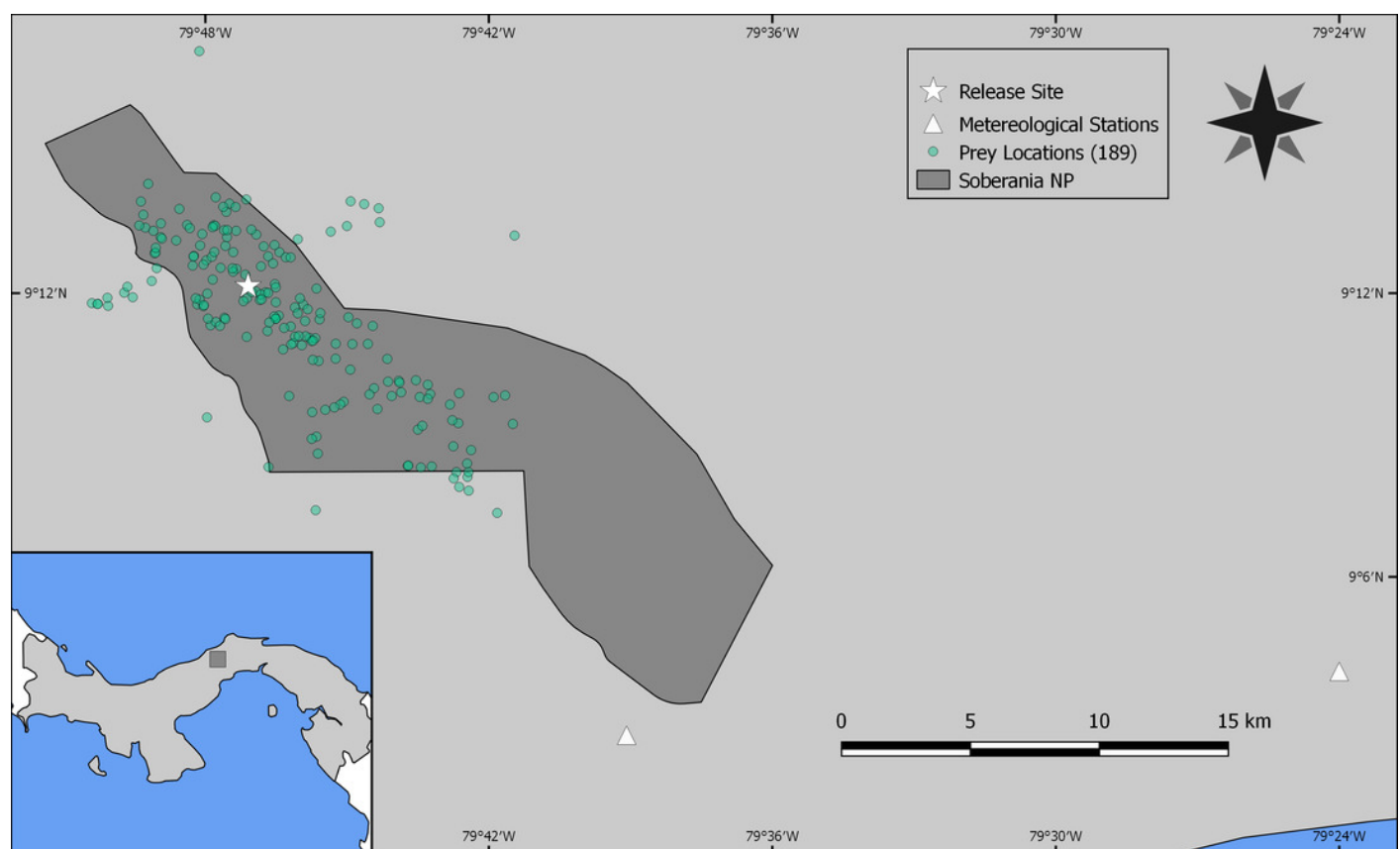



Figure 3

Fig. 3. Prey composition and effort.

Monthly distribution of harpy eagle kills throughout the year. Vertical bars are color-coded according to the main prey functional groups. Observations were made in all months of the year, however more scantly in November.

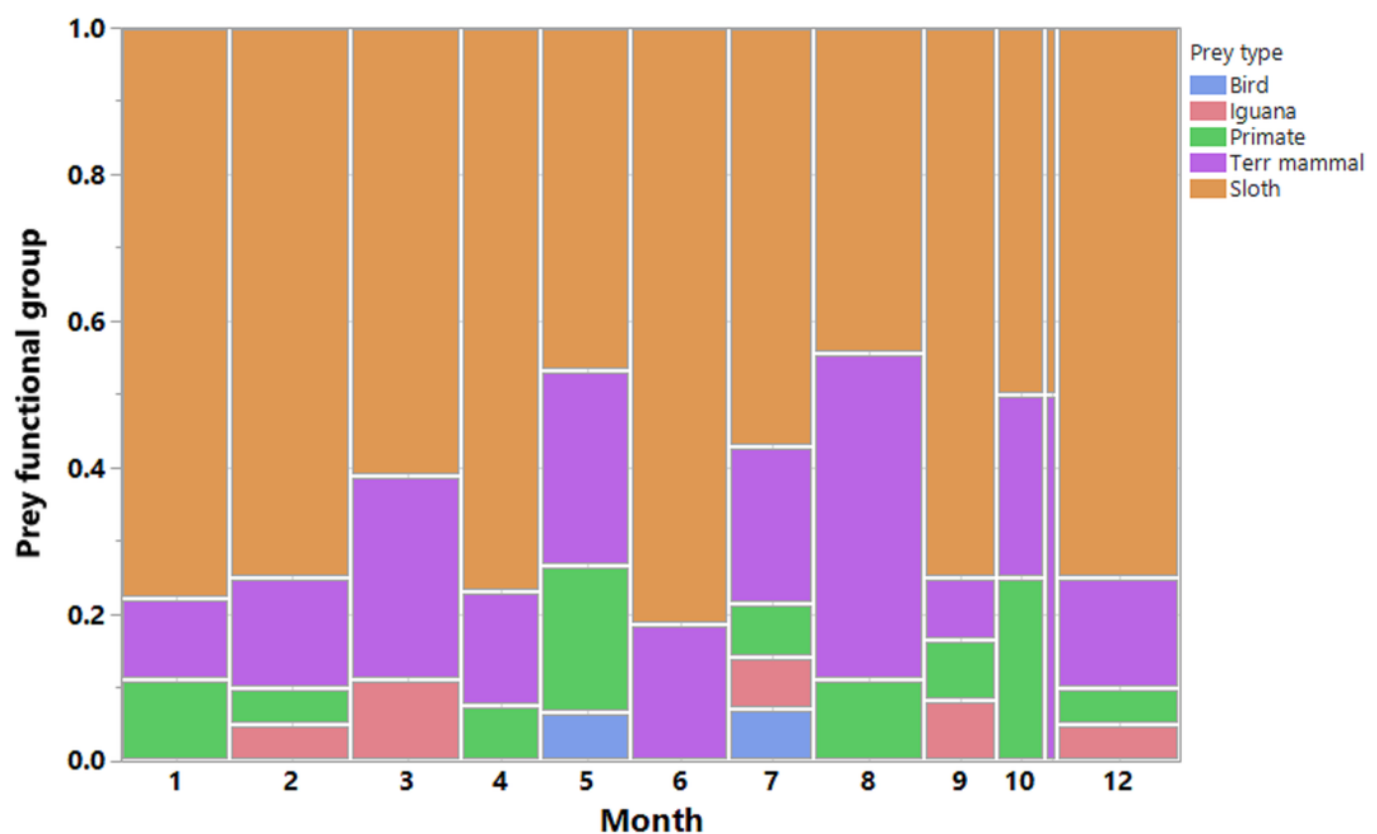
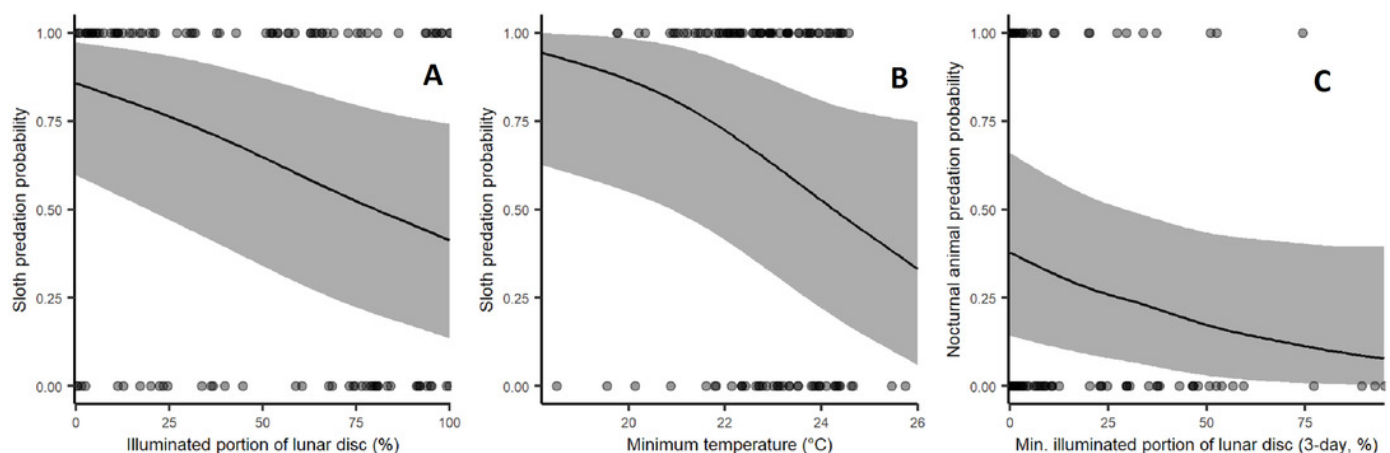



Figure 4

Effect of environmental variables on the probability of predation events by harpy eagles.

A - Effect of moon brightness on sloth predation probability: fewer sloths were taken during bright moonlit nights (p = 0.0134). B - Effect of minimum temperature on sloth predation probability: fewer sloths were taken under cooler conditions (p = 0.0413). C - Effect of moon brightness on nocturnal mammal predation: fewer nocturnal prey were killed.during bright nights, but this lacked statistical significance (p = 0.12).

Variables used in the models

Climatic variables used in mixed generalized linear models (GLMM) explaining the dietary profile of harpy eagles. Each GLMM is used to predict the probability that a given prey item belongs to the response variable. 'Normalized difference vegetation index' (NDVI) is a proxy for deciduousness, calculated using data from LANDSAT imagery. All other climatic variables were obtained from meteorological stations near the study site. Variables noted as '3-day' are pooled over a three-day period up to any given prey detection event.-

1   **Table 1. Variables used in the models.**

2   Climatic variables used in mixed generalized linear models (GLMM) explaining the dietary

3   profile of harpy eagles. Each GLMM is used to predict the probability that a given prey item

4   belongs to the response variable. 'Normalized difference vegetation index' (NDVI) is a proxy for

5   deciduousness, calculated using data from LANDSAT imagery. All other climatic variables were

6   obtained from meteorological stations near the study site. Variables noted as '3-day' are pooled

7   over a three-day period up to any given prey detection event.-

Explanatory Variables	Response Variable	
	Sloth	Nocturnal
NDVI	X	X
Cumulative rainfall (3-Day; mm)	X	
Rainfall (mm)	X	
Minimum temperature (3-Day; °C)	X	
Minimum temperature (°C)	X	
Maximum temperature (°C)	X	
Lunar disc (%)	X	X
Maximum lunar disc (3-Day; %)		X
Minimum lunar disc (3-Day; %)		X
Deciduousness*Maximum lunar disc	X	X
Cumulative rainfall*Minimum temperature (3-day)	X	

Prey composition in the diet of harpy eagles.

Seasonal changes in incidence of kills by harpy eagles shown in percentages, combining frequencies for both wet and dry seasons across the seven years of study (2003 – 2009). Overall column shows percentages of prey items for all periods combined, and sample sizes (in parentheses). See "Study Site" section of Methods for further details of season definition.

1   **Table 2. Prey composition in the diet of harpy eagles.**

2   Seasonal changes in incidence of kills by harpy eagles shown in percentages, combining

3   frequencies for both wet and dry seasons across the seven years of study (2003 – 2009). Overall

4   column shows percentages of prey items for all periods combined, and sample sizes (in

5   parentheses). See "Study Site" section of Methods for further details of season definition.

Species	Dry %	Wet %	Overall % (n)
Brown-throated sloth *Bradypus variegatus*	36.8	31.4	34.1 (59)
Hoffmann's two-toed sloth *Choloepus hoffmanni*	24.1	7.0	15.6 (27)
Unidentified sloths	11.5	19.8	15.6 (27)
White-nosed coati *Nasua narica*	5.7	9.3	7.5 (13)
Northern lesser anteater *Tamandua mexicana*	2.3	11.6	6.9 (12)
Mantled howler monkey *Alouatta palliata*	3.4	7.0	5.2 (9)
Green Iguana *Iguana iguana*	4.6	2.3	3.4 (6)
Common opossum *Didelphis marsupialis*	2.3	2.3	2.3 (4)
White-headed capuchin *Cebus capucinus*	2.3	2.3	2.3 (4)
Collared peccary *Tayassu tajacu*	1.1	2.3	1.7 (3)
Nine-banded armadillo *Dasypus novemcinctus*	1.1	1.2	1.1 (2)
Central American agouti *Dasyprocta punctata*	2.3	0.0	1.1 (2)
Crab-eating raccoon *Procyon cancrivorus*	1.1	0.0	0.5 (1)
Tayra *Eira Barbara*	1.1	0.0	0.5 (1)
Black vulture *Coragyps atratus*	0.0	1.2	0.5 (1)
Unidentified parrot	0.0	1.2	0.5 (1)

| Unidentified monkey | 0.0 | 1.2 | 0.5 (1) |