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

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23 Running header: Sloth predation by harpy eagles
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26 **Abstract**

27 **Background**. Climate plays a key role in the life histories of tropical vertebrates. However,

28 tropical forests are only weakly seasonal compared with temperate and boreal regions. For

29 species with limited ability to control core body temperature, even mild climatic variation can

30 determine major behavioural outcomes, such as foraging and predator avoidance. In tropical

31 forests, sloths are the arboreal vertebrate attaining the greatest biomass density, but their capacity

32 to regulate body temperature is limited, relying on behavioural adaptations to thermoregulate.

33 Sloths are largely or strictly nocturnal, and depend on crypsis to avoid predation. The harpy

34 eagle (*Harpia harpyja*) is a sloth-specialist and exerts strong top-down control over its prey

35 species. Yet the role of environmental variables on the regulation of predator-prey interactions

36 between sloths and harpy eagles are unknown. The harpy eagle is considered Near Threatened.

37 This motivated a comprehensive effort to reintroduce this species into parts of Mesoamerica.

38 This effort incidentally enabled us to understand the prey profile of harpy eagles over multiple

39 seasons.

40 **Methods**. Our study was conducted between 2003 and 2009 at Soberanía National Park (SNP),

41 Panamá. Telemetered harpy eagles were seen hunting and feeding on individual prey species.

42 For each predation event, field assistants systematically recorded the species killed. We analysed

43 the effects of climatic conditions and vegetation phenology on the prey species profile of harpy

44 eagles using generalised linear mixed models.

45 **Results**. Here we show that sloth predation by harpy eagles was negatively affected by nocturnal

46 ambient light (i.e. bright moonshine) and positively affected by seasonally cool temperatures. We

47 suggest that the first ensured low detectability conditions for sloths foraging at night and the

48 second posed a thermally unsuitable climate that forced sloths to forage under riskier daylight.

49 We showed that even moderate seasonal variation in temperature can influence the relationship

50   between a keystone tropical forest predator and a dominant prey item. So predator-prey ecology

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

52   effects shown here suggest important demographic consequences for sloths, which are under top-

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

54   higher latitudes.

55

56

Introduction

57

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

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

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

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

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

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

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

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

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

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

68 2015), there are relatively few studies about the nature of such effects on predator-prey

69 interactions.

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

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

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

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

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

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

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

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

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

79 2016). Therefore, they need to bask and can be affected by even mild variation in habitat cover

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

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

82   2014).

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

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

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

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

87   (~4kg; Wetzel & Montgomery, 1985), have a relatively low body temperature (Vendl et al.,

88   2016), and feed on leaves exclusively (Dill-McFarland et al., 2016). Finally, two-toed sloths

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

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

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

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

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

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

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

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

97   and therefore are less likely to suffer predation.

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

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

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

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

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

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

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

105 this lack of knowledge almost impossible to overcome.

106   The harpy eagle (*Harpia harpyja*; Fig 1) is considered Near Threatened by the IUCN

107 (Birdlife International, 2017), mainly because of human persecution (Muñiz-López, 2017) and

108 habitat loss, which have extirpated these mega-raptors from 41% of their former historical range

109 distribution (Miranda et al., 2019). Harpy eagles are an apex predator that specialises on sloths,

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

111 2014; Miranda, 2015). Harpy eagles hunt passively by visually scanning and listening to the

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

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

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

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

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

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

118 The Peregrine Fund has lead a comprehensive effort to reintroduce this species into parts of

119 Mesoamerica (Campbell-Thompson et al., 2012; Watson et al., 2016). This effort, spanning from

120 2003 to 2009, incidentally enabled us to understand, for the first time, the prey profile of harpy

121 eagles over multiple seasons.

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

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

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

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

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

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

128   would increase with low moon brightness.

129

Materials & Methods

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

149 (43 km from the release site). A Walter-Lieth climate diagram describing the seasonality of

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

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

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

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

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

155 (2012) and Watson et al. (2016). Harpy eagles were fitted with both radio-telemetry and GPS

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

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

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

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

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

161 eagle was required to check its body condition.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

182   observations were typically sparser during the month of November.

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

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

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

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

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

188   the normalised difference vegetation index (NDVI) as a proxy for canopy leaf deciduousness,

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

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

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

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

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

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

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

196   metric for the detection date of each prey item.

197   We ran two batches of generalised linear mixed-effects models (GLMM) using as

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

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

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

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

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

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

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

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

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

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

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

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

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

211

Results

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

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

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

216   88 prey samples during the dry seasons and 85 samples during the wet seasons. The temporal

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

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

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

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

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

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

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

224   in Table 1.

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

226   0.0116) and low ambient temperatures with marginal statistical significance ($\beta = -0.508$, p =

227   0.0535; Fig. 4). Harpy predation on nocturnal animals was weakly affected by low moon

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

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

230   are summarised in Table 2.

231

Discussion

232

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

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

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

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

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

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

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

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

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

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

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

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

245 and anticipate their attacks with evasive maneuvers may increase foraging activity under high

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

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

248 presence (Voirin et al., 2014), and in other areas generally showing greater fear of diurnal

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

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

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

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

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

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

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

256   55% of all attacked sloths are successfully killed, while only 33% of visually oriented prey are

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

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

259   foraging time, neutralising search images of diurnal predators and greatly reducing their

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

261   confirmatory evidence.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

289   effects on predation of sloths. Although we predicted increased probability of arboreal prey

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

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

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

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

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

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

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

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

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

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

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

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

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

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

304   2014). The harpy eagle sit-and-wait predation strategy is further enhanced by their retractable

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

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

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

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

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

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

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

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

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

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

315   question.

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

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

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

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

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

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

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

323   Forest needs careful evaluation.

324

Conclusions

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

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

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

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

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

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

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

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

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

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

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

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

338 would help fill this knowledge gap.

339

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352

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481

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).
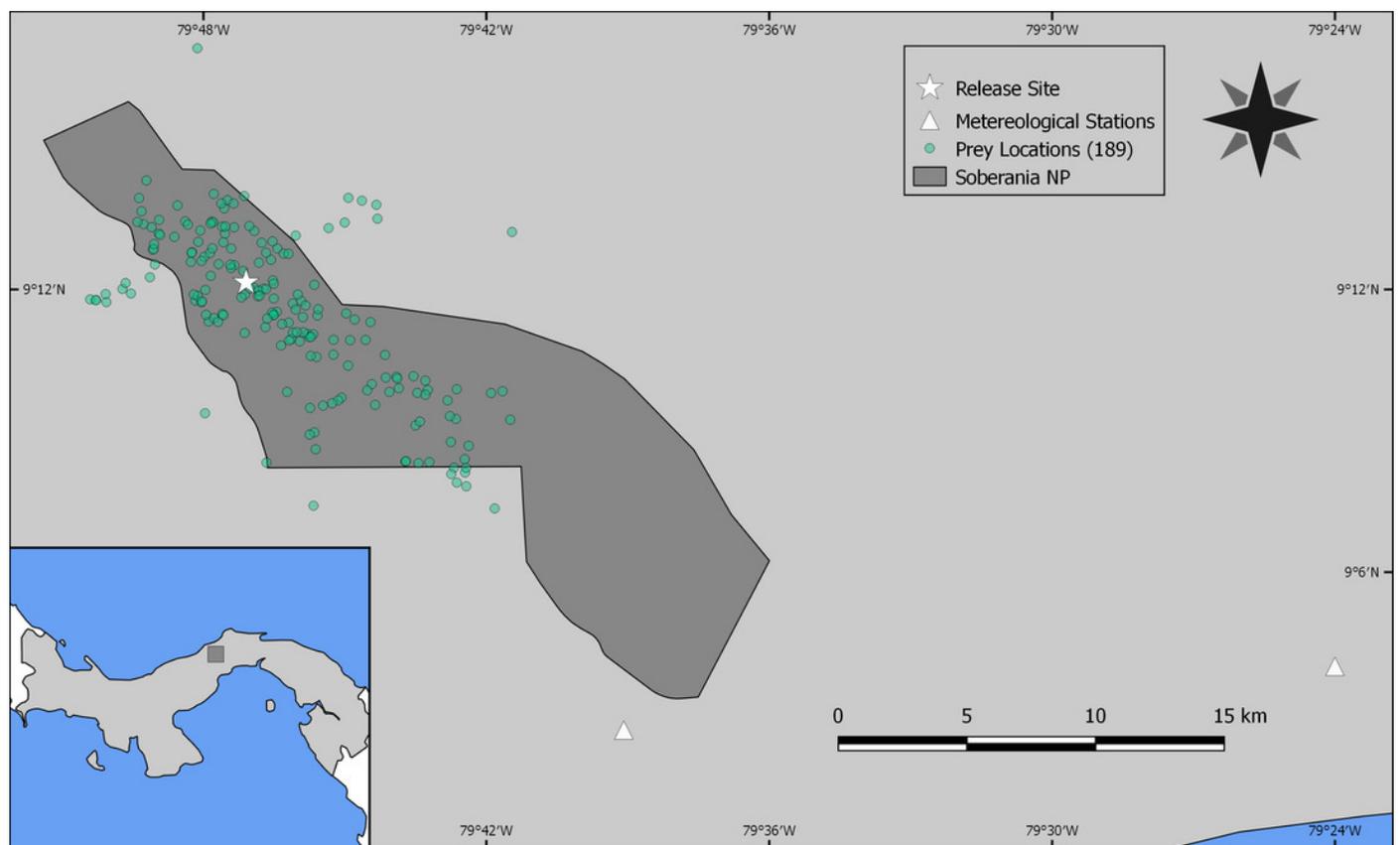
Figure 3

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.
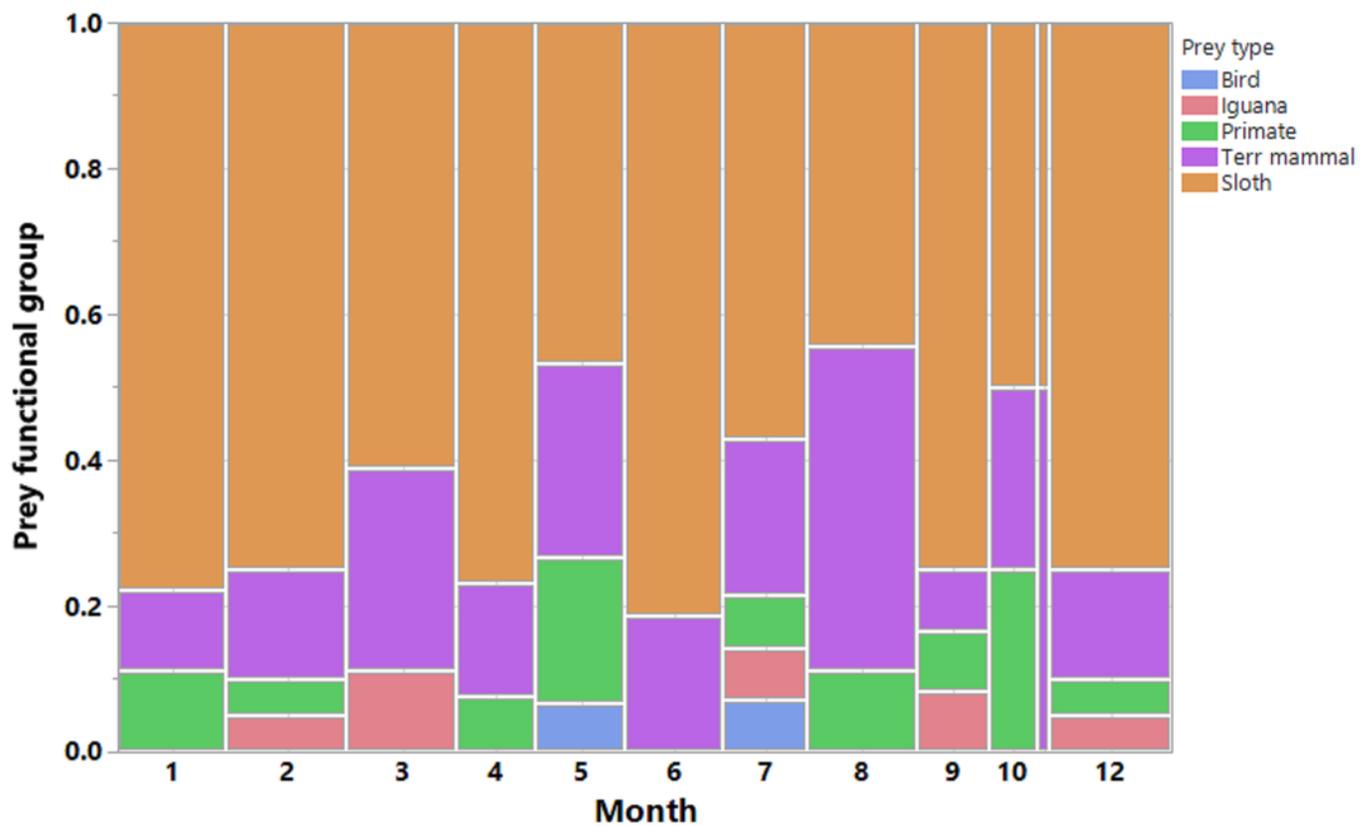
Figure 4

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).
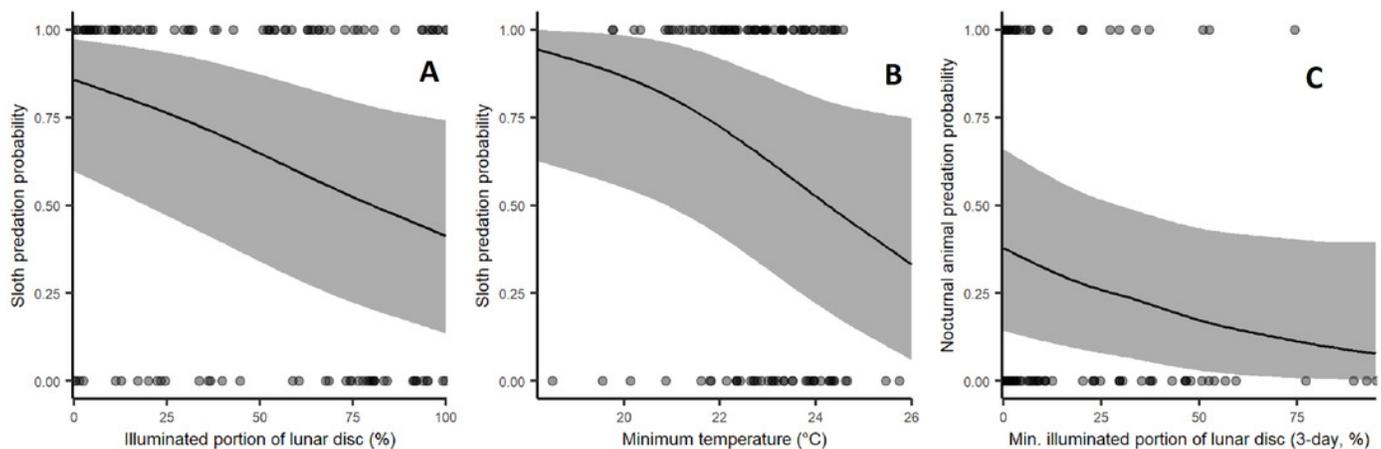
Table 1. Prey composition in the diet of harpy eagles.

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 1. 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) |

Table 2. Results of generalized linear mixed models of harpy eagle prey profile.

First model predicts probability that a given animal preyed by a harpy eagle is a sloth, while the second model predicts probability of prey being a nocturnal animal. Both models use a logit link due to the binomial natural of the data. Both models use tracked individuals and years sample as random effects over the intercept.

1   **Table 2. Results of generalized linear mixed models of harpy eagle prey profile.** First model

2   predicts probability that a given animal preyed by a harpy eagle is a sloth, while the second model

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4   binomial natural of the data. Both models use tracked individuals and years sample as random

5   effects over the intercept.

Model	Variable	Estimate	Standard Error	p-value	Random Individual Variance	Random Yearly Variance
Sloth	Intercept	0.588	0.470	0.2109	1.001	0.513
	Lunar disc (%)	-0.648	0.257	0.0116	-	-
	Minimum temperature (°C)	-0.508	0.263	0.0535	-	-
Night	Intercept	-0.933	0.422	0.0271	0.336	0.367
	Minimum lunar disc (3-Day; %)	-0.392	0.269	0.1461	-	-