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13 **Quantifying the scale and socioeconomic drivers of bird hunting in Central African forest**  
14 **communities**

15

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52 **Abstract**

53 Global biodiversity is threatened by unsustainable exploitation for subsistence and commerce, and  
54 tropical forests are facing a hunting crisis. In Central African forests, hunting pressure has been  
55 quantified by monitoring changes in the abundance of affected species and by studying wild meat  
56 consumption, trade and hunter behaviour. However, a proportion of offtake is also discarded as  
57 bycatch or consumed by hunters when working, which can be overlooked by these methods. For  
58 example, remains of hornbills and raptors are found regularly in hunting camps but relatively few  
59 birds are consumed in households or traded in markets. Hornbill and raptor populations are  
60 sensitive to small increases in mortality because of their low intrinsic population growth rates,  
61 however, the scale and socioeconomic drivers of the cryptic hunting pressure affecting these species  
62 have not been quantified. We used direct and indirect questioning and mixed-effects models to  
63 quantify the socioeconomic predictors, scale and seasonality of illegal bird hunting and consumption  
64 in Littoral Region, Cameroon. We predicted that younger, unemployed men with low educational  
65 attainment (i.e. hunters) would consume birds more often than other demographics, and that  
66 relative offtake would be higher than expected based on results from village and market-based  
67 studies. We found that birds were primarily hunted and consumed by unemployed men during the  
68 dry season but, in contrast to expectations, we found that hunting prevalence increased with  
69 educational attainment. Within unemployed men educated to primary level (240 of 675 respondents  
70 in 19 villages), we estimated an average of 29 hornbills and eight raptors (compared with 19  
71 pangolins) were consumed per month during the study period (Feb - Jun 2015) in a catchment of  
72 c.1,135 km<sup>2</sup>. We conclude that large forest birds face greater hunting pressure than previously  
73 recognised, and birds are a regular source of protein for men during unemployment. Offtake levels  
74 may be unsustainable for some raptors and hornbills based on life history traits but in the absence of  
75 sufficient baseline ecological and population data we recommend that a social-ecological modeling  
76 approach is used in future to quantify hunting sustainability.

77

78

79 **Introduction**

80 Overexploitation is the greatest immediate threat to global biodiversity (Maxwell et al. 2016;  
81 Benítez-López et al. 2017) and a growing hunting crisis threatens forest species, ecosystems and  
82 food security in Asia, Africa and South America (Milner-Gulland & Bennett 2003; Abernethy et al.  
83 2013; Ripple et al. 2016; Benítez-López et al. 2017). For affected taxa, the direct consequences of  
84 excessive hunting are population declines and, in some cases, extirpation (Maisels et al. 2001). The  
85 indirect consequences are manifold and include the disruption of trophic cascades, reduced  
86 ecosystem functioning and changes in forest structure (Abernethy et al. 2013). For example, hunting  
87 of frugivorous birds and monkeys in Brazil's Atlantic rainforest reduced carbon storage capacity  
88 through the disruption of seed dispersal processes (Culot et al. 2017). Unsustainable hunting can  
89 therefore have wide reaching consequences for ecosystems and people who rely on forest resources  
90 for subsistence and commerce.

91 In Central and West Africa, where bushmeat (hereafter 'wild meat'; Milner-Gulland &  
92 Bennett 2003) hunting is ubiquitous, there has been a focus on quantifying offtake of commercially  
93 valuable taxa, with an emphasis on the trade and consumption of large-bodied mammals (Fa et al.  
94 2000; Brashares et al. 2004; Cowlishaw et al. 2005; Fa et al. 2006; Supplementary Material in  
95 Benítez-López et al. 2017). However, the focus on commercial markets may have underestimated  
96 the diversity and abundance of hunted species because bycatch and local consumption (e.g. in  
97 villages or by hunters) is overlooked. Consequently, offtake of other less valuable taxa may have  
98 been underestimated (Trail 2007; Fa et al. 2011). Extensive surveys of wild meat markets in Ghana  
99 failed to detect large-scale hunting of fruit bats (Kamins et al. 2011) and in Cameroon relatively few  
100 birds are sold in markets (Fa et al. 2006) but birds are killed regularly by hunters (Whytock et al.  
101 2016). In West Africa, raptors are sold as 'fetish' for use in traditional medicine, witchcraft and as  
102 wild meat (Buij et al. 2016), but total numbers are low relative to mammals (e.g. in Nigeria: Fa et al.  
103 2006), and this may have led to complacency over the threat that hunting poses to birds in the  
104 region.

105           It is widely acknowledged that hunting threatens game birds, hornbills and raptors in Asian  
106 and South American tropical forests (e.g. Thiollay 2005; Dasgupta & Hilaluddin 2012; Beastall et al.  
107 2016), but evidence from Central and West Africa is equivocal. In the Republic of Congo and Gabon,  
108 hunting had a minimal effect on hornbills relative to mammals, and hunting appeared to indirectly  
109 ‘benefit’ some frugivorous hornbills due to competitive release (Poulsen et al. 2011; Koerner et al.  
110 2017). In contrast, White-breasted Guineafowl abundance was lower in hunted forests in the Ivory  
111 Coast (Walter et al. 2010). Improved access to firearms in recent years may have made birds and  
112 arboreal mammals more accessible to hunters in Central Africa, and demand for smaller taxa such as  
113 rodents and birds is expected to increase when populations of large-bodied mammals decline (Fa et  
114 al. 2000; Cowlshaw et al. 2005). Thus, even if birds have not historically been threatened by hunting  
115 pressure, hunting regime shifts could now pose a threat, particularly in heavily hunted areas  
116 (Benítez-López et al. 2017).

117           Rodents and small mammals such as blue duiker *Philantomba monticola* can tolerate high  
118 levels of hunting pressure (Cowlshaw et al. 2005), but hornbills and other relatively large-bodied  
119 birds are vulnerable to over-exploitation due to their slow life histories (Owens & Bennett 2000;  
120 Thiollay 2005; Sreekar et al. 2015). Known hunted species in Central Africa such as black-casqued  
121 hornbill *Ceratogymna atrata* and palm-nut vulture *Gypohierax angolensis* have low fecundity,  
122 producing a maximum of one (rarely two) offspring per annum, and population densities are  
123 intrinsically low (Stauffer & Smith 2004). Declines of other large-bodied birds with similar life-history  
124 traits also provide forewarning, and Africa’s savannah vulture populations have undergone recent,  
125 continent-wide declines due to persecution and hunting for belief-based use and meat consumption  
126 (Ogada et al. 2015).

127           Contrary to SE Asia and S America, where commercial bird hunting is common (Thiollay  
128 1984; Thiollay 2005; Beastall et al. 2016), in Africa the international and local trade of hornbill body  
129 parts is relatively small or almost non-existent, and hornbill skulls, feathers and other body parts are  
130 regularly discarded as wastage in forest hunting camps (e.g. in Cameroon). This suggests that,

131 although hunting does occur, birds have relatively low commercial value (Whytock et al. 2016).  
132 Actually, hunters might consume birds instead of commercially valuable meat when working from  
133 forest camps, thus maximising profits (Whytock et al. 2016). However, hunters are reluctant to  
134 discuss potentially illegal activities for fear of recrimination, and establishing the scale and drivers of  
135 this cryptic, non-commercial hunting pressure is therefore challenging.

136 Here, we combined direct and indirect questioning, which gives respondents anonymity and  
137 prevents self-incrimination (Unmatched Count Technique: Nuno et al. 2013; Nuno & St John 2015),  
138 to quantify the scale, seasonality and socioeconomic drivers of bird hunting and consumption in  
139 Littoral Region, Cameroon. For comparison, we also quantified consumption of small mammals to  
140 compare relative offtake levels. Based on previous work in our study area, which found a relatively  
141 high number of bird remains discarded in forest hunting camps (Whytock et al. 2016), we expected  
142 that (1) birds would be hunted and consumed by younger, unemployed males with low educational  
143 attainment (i.e. the assumed demographic of hunters in our study area), and (2) bird offtake would  
144 be higher than estimated by market and village-based studies, assuming that most birds are  
145 consumed in the forest by hunters rather than sold commercially or extracted to villages.

146

## 147 **Methods**

### 148 ***Study area***

149 Nineteen villages were surveyed in the Nkam and Sanaga Maritime departments of Cameroon's  
150 Littoral Region. Villages bordering the proposed Ebo National Park that use the forest for hunting  
151 were selected for surveys (ENP; Fig. 1). The ENP (c. 1,135 km<sup>2</sup>) is characterised by lowland and sub-  
152 montane closed canopy forest, with subsistence farming and oil-palm plantations at its edge  
153 (Morgan 2008).

154 The Ebo Forest Research Project was established in 2005 and conducts a permanent  
155 programme of conservation research and education in the ENP and its surroundings. Local  
156 communities are therefore familiar with basic wildlife law in Cameroon. There has also been a high-

157 profile increase in wildlife law enforcement in Cameroon during the past decade (Last Great Ape  
158 Organisation 2014) and very few hunters are thought to have the legal permits required to hunt  
159 wildlife or own a firearm (quantitative data unavailable). Hunters are therefore reluctant to discuss  
160 their activities for fear of prosecution.

161

### 162 ***Bird hunting prevalence***

163 To quantify bird hunting prevalence, we used the Unmatched Count Technique (UCT: Droitcour  
164 1991), which has been successfully used to quantify illegal hunting prevalence in East and Central  
165 African hunting communities (Nuno et al. 2013; Harrison et al. 2015; Nuno & St John 2015). We  
166 approached potential respondents  $\geq 18$  years old and asked if they would like to participate. A coin  
167 toss was used to randomly assign consenting respondents to a treatment or control group. We then  
168 used a scripted questionnaire (Supplementary Material) to record demographic variables (gender,  
169 age, place of upbringing, educational attainment and employment status) before asking two UCT  
170 questions, which were (1) How many of these activities do you do in the dry season? and (2) How  
171 many of these activities do you do in the wet season? The control UCT list included four non-  
172 sensitive activities, which were 'transport commercial timber', 'buy from the market', 'farm work'  
173 and 'construction work' and the treatment UCT list included the additional sensitive activity 'hunt  
174 birds with a slingshot or gun'. Questionnaires, historic census data for the study area and additional  
175 information on the UCT method are given in Supplementary Material.

176 The UCT is dependent on respondents' understanding and willingness to participate. We  
177 therefore asked respondents if the questionnaire was easy to understand, if they felt anonymous,  
178 and if they felt comfortable answering the questions. The interviewer also assessed how well  
179 respondents understood the interview, how willing they were to participate, and if they were  
180 perceived to be honest.

181 Surveys were conducted from February to June 2015, partially covering the dry and wet  
182 seasons, from Feb – Mar and Apr – Jun, respectively. A total of 789 people was approached in 19

183 villages, and ten individuals (1.27%) declined to participate. We excluded questionnaires with  
184 missing data, leaving a sample size of  $n = 675$  questionnaires ( $n = 136$  female control,  $n = 156$  female  
185 treatment;  $n = 167$  male control,  $n = 216$  male treatment). The mean number of respondents  
186 questioned per village was  $35.5 \pm 7.7$  SE, and the mean number of interviews per month was  $135$   
187  $\pm 47.9$  SE. Interviews lasted for a median of 7 minutes (range 1 – 25, Q1 = 4, Q3 = 10 minutes).  
188 Summary statistics for all questionnaire data are given in Table S1.

189

### 190 ***Bird consumption***

191 Although illegal hunting activities are considered sensitive, *consuming* wild meat is generally  
192 considered non-sensitive. For example, confiscated meat is auctioned to the public by authorities for  
193 consumption rather than wasted, and many common taxa (e.g. tree pangolin *Phataginus tricuspis*)  
194 are openly consumed in villages and restaurants without fear of recrimination. We therefore used  
195 direct questioning to estimate bird consumption. We also quantified consumption of small mammals  
196 to allow us to compare bird offtake relative to better-studied species.

197         Respondents were asked to estimate the number of meals in the past week (none, 1 – 5, 6 –  
198 10 or > 10) that contained meat from seven wild meat species or groups ( $n = 4$  birds,  $n = 3$   
199 mammals). The list included three bird species considered vulnerable to hunting pressure because of  
200 their large body size (Ingram et al. 2015) and that have been recorded by previous wild meat studies  
201 in Cameroon (Whytock et al. 2013); palm-nut vulture, black-casqued hornbill and white-thighed  
202 hornbill *Bycanistes albotibialis*. These were also considered easy to identify using local names. A  
203 fourth bird group, ‘eagle’, was included to cover large raptors that were considered difficult for  
204 respondents to accurately identify to species level (i.e. Cassin’s hawk eagle *Aquila africana*, crowned  
205 eagle *Stephanoaetus coronatus*, European honey buzzard *Pernis apivorus* and African harrier hawk  
206 *Polyboroides typus*). The list of mammals included three species’ groups (squirrel, rat, and arboreal  
207 pangolins) chosen because they are openly consumed throughout the study area.

208



209 ***Ethics statement***

210 We followed the Code of Ethics of the American Anthropological Association 2009. Before answering  
211 the questionnaire, all respondents were given a clear explanation of the study's purpose and asked if  
212 they would like to participate (Supplementary Material). All data were collected anonymously, and  
213 the names of participating villages have been anonymised to reduce ethical concerns (St John et al.  
214 2016). No formal ethics approval was received as the study was conceived and funded  
215 independently, but it was judged to be ethically sound by reviewers of funding applications and by  
216 collaborators from the authors' respective institutions. Research was conducted with permission  
217 from Cameroon's Ministry of Scientific Research and Innovation, permit number  
218 045/MINRESI/B00/C00/C10/nye.

219

220 **Data analysis**

221 ***Bird hunting prevalence***

222 We used linear mixed effects models to analyse UCT data. The baseline, average hunting prevalence  
223 in the population was first estimated for each UCT question by including card type (treatment or  
224 control) as a fixed effect and  $n$  list items as the response. Village was included as a random intercept  
225 to account for pseudoreplication ( $n = 19$  villages). Prevalence was calculated as the percentage  
226 change from the intercept (control card) to the estimate for the treatment card ( $n = 675$   
227 respondents).

228 For each UCT question, we examined the effects of gender, age, place of upbringing,  
229 educational attainment and employment status on the response ( $n$  list items) by constructing  
230 models with two-way interactions between card type (treatment or control) and each demographic  
231 variable to calculate the prevalence of the sensitive activity. Village was included as a random  
232 intercept to account for pseudoreplication. We also initially included  $n$  years in the current village as  
233 a fixed effect but it was highly correlated with age ( $r = 0.63$ ), and since the effects of these two  
234 variables would likely be indistinguishable in the model only age was retained in the analysis.

235 To select the 'best' demographic model we generated all possible fixed effect combinations  
236 and compared model fit using corrected Akaike Information Criterion (AICc) (Burnham & Anderson  
237 2002). Models were only considered where interactions between card type and demographic  
238 variables were present alongside their constituent main effects ( $n = 33$  models). Confidence intervals  
239 (95%) were bootstrapped from 500 re-samples. Where confidence intervals did not include zero this  
240 was considered strong evidence of an effect and its direction.

241 A key assumption of the UCT is that the addition of the sensitive item in the treatment list  
242 does not influence the way in which participants respond to the control items (design effect). We  
243 tested for this using the `ict.test` function in the R package `list` (Blair & Imai 2010) before conducting  
244 analyses, finding no evidence of an effect ( $H_0 = \text{no design effect}, P > 0.05$ ).

245

#### 246 ***Bird and mammal consumption***

247 Most respondents indicated that relatively few meals (none or 1 - 5) per week contained meat from  
248 a given species (Fig. S1), and we modelled the effects of season and demographic variables on wild  
249 meat consumption using a binomial generalised linear mixed effects model. A global model was  
250 constructed with wild meat (i.e. birds and mammals combined) consumed in the past week (yes or  
251 no) as the response variable (7 species x 675 respondents =  $n$  4725 yes or no answers), month (i.e.  
252 month of questioning) as a categorical fixed effect and demographic variables as categorical fixed  
253 effects (other than age, which was continuous). Species and village were included as random  
254 intercepts. The full model did not converge and we chose to exclude place of upbringing to reduce  
255 the model's complexity, and because most individuals originated from the Littoral Region (Table S1).  
256 To quantify how demographic factors differentially affected bird and mammal consumption, we  
257 included two-way interactions between each of the demographic variables and a binary categorical  
258 variable 'bird or mammal', expecting mammals to be consumed more often than birds in the general  
259 population. The best model was selected using  $\Delta\text{AICc}$  as described for the UCT analysis, with the  
260 criteria that demographic factors were only considered alongside their interactions, and likewise

261 interactions were not considered without their constituent main effects. This constrained the total  
262 number of possible models to  $n = 32$ . To estimate the probability of consuming a given species we  
263 extracted the conditional modes of the intercept from the random intercept term for species.

264 Conditional modes of the intercept were also used to estimate the number of carcasses  
265 consumed per month by the most common class of respondent in the dataset (unemployed male  
266 educated to primary level,  $n = 240$  individuals). This was done by first calculating the total number of  
267 meals consumed per week for each species based on consumption probability estimates, then  
268 multiplying the result by 50. This was assuming 50 g of meat per day based on Cameroon's per capita  
269 meat carcass availability in 2013 (14.5 kg per person per year or approximately 40 g of meat per day)  
270 from the Food and Agriculture Organization of the United Nations' data ([www.fao.org/faostat](http://www.fao.org/faostat)). We  
271 adjusted this figure to 50 g because meat consumption in our study area (forest zone) is likely to be  
272 higher than the average in Cameroon, which includes data from the Sahel. The final figure was  
273 extrapolated to estimate the total number of carcasses consumed per month based on average body  
274 mass estimates (Table S2) for each species or group (body mass estimates were taken from Fa et al.  
275 2006 for mammals and del Hoyo et al. 2016 for birds). For 'rat' we used the body mass estimate for  
276 giant pouched rat *Cricetomys* sp. and for 'eagle' we averaged the mean adult body mass of Cassin's  
277 hawk eagle, crowned eagle, European honey buzzard and African harrier hawk. For pangolins, we  
278 used the body mass estimate for tree pangolin. R statistical software and the lme4 and MuMIn  
279 packages were used for analyses (Barton 2015; Bates et al. 2015; R Core Team 2015).

280

## 281 **Results**

### 282 ***Bird hunting prevalence***

283 Bird hunting was a dry season activity and prevalence increased with educational attainment (Fig. 2,  
284 Fig. S2, Tables S3 & S4), reaching 12.1% in respondents educated to secondary level or above ( $n =$   
285 142 respondents). Models that included other demographic variables had little support (Tables S3 &  
286 S4).

287 ***Bird and mammal consumption***

288 Probability of wild meat consumption (i.e. mammals and birds combined) in the previous week was  
289 best explained by the full model that included interactions between taxa (bird or mammal) and each  
290 of the demographic variables (age, employment status, education level, gender and month) (Tables  
291 1 & S5 Fig. 3). As expected, mammals were consumed more often than birds (Fig. 3).

292 Mammal consumption increased slightly with age although the effect was small (Table 1),  
293 and age had almost no detectable effect on bird consumption (Figs. 3a & 3b). We detected a weak  
294 relationship between educational attainment and mammal consumption, but the interaction  
295 between educational attainment and taxa showed that bird consumption was significantly lower  
296 when respondents were educated to secondary level or above, which contradicted results from the  
297 unmatched count technique (Figs. 3c & 3d). For both birds and mammals, the main effect of  
298 employment status showed that consumption was lower when respondents were employed (Figs. 3e  
299 & 3f).

300 In agreement with expectations, bushmeat (birds and mammals combined) was consumed  
301 more often by men. The interaction between taxa and gender showed that the difference in  
302 consumption between men and women was more extreme for birds, although the effect was  
303 marginally non-significant (Figs. 3g & 3h; Table 1). Seasonally, the probability of consuming both  
304 birds and mammals declined as the wet season progressed from February to May, before peaking  
305 again in June (Figs. 3i & 3j). The interaction between taxa and month showed that bird and mammal  
306 consumption did not differ significantly in February and June, but mammals were consumed more  
307 frequently in March, April and May.

308

309 ***Offtake estimates for individual species or groups***

310 Among birds, hornbills were consumed in the greatest numbers, with an estimated average of  
311 approximately 17 black-casqued hornbills and 12 white-thighed hornbills consumed per month in  
312 the catchment by the 240 unemployed males educated to primary level (Fig. 4). Raptors were

313 consumed in lower numbers by this demographic, with an average of seven palm-nut vultures and  
314 one 'eagle' consumed per month. Squirrels were the most frequently consumed mammal in this  
315 group of respondents, followed by rats and pangolins, respectively (Fig. 4).

316

### 317 ***Respondent understanding***

318 All respondents found the interview easy to understand and 99% felt anonymous. For respondent  
319 comfort, 60.6% felt uncomfortable after answering questions. This was close to expectations given  
320 that 55.1% of respondents were shown the treatment card with the illegal activity. The interviewer  
321 also reported high levels of perceived comprehension, willingness to answer and honesty (Table S1).

322

### 323 **Discussion**

324 Results show that bird hunting and consumption are widespread and occur at relatively high levels in  
325 Cameroon's Littoral region, and estimated annual offtake exceeds that estimated by previous  
326 surveys of hunting camp wastage, wild meat sales and village offtake (c.f. Table 1 in Whytock et al.  
327 2016). Evidence from hunting camp surveys ( $n = 13$  camps surveyed for one year) suggested that  
328 approximately two white-thighed hornbills and 1.5 black-casqued hornbills are killed per month in  
329 the ENP on average (Whytock et al. 2016). In contrast, our results indicate these figures could be as  
330 high as 12 and 17 individuals per month, respectively, based on the estimated numbers consumed  
331 by 240 male respondents (36% of 675 total respondents). Despite these high offtake levels, relatively  
332 few hornbills have been recorded as wild meat in Cameroon and elsewhere in Central Africa  
333 (Abernethy et al. 2013; Supplementary Material in Benítez-López et al. 2017), thus highlighting the  
334 low-profile and hidden nature of bird hunting in the region. More generally, relative offtake  
335 estimates showed that during some months (particularly February and June) unemployed men  
336 consumed black-casqued hornbills and white-thighed hornbills as often as rats and pangolins (Fig. 4),  
337 indicating that wild birds are an important source of protein for this demographic.

338 Previous research in the ENP suggested that hunters consume birds instead of commercially  
339 valuable species in forest camps (Whytock et al. 2016), perhaps to maximise profits. This is  
340 supported by our results, which show that birds are rarely consumed by educated women in  
341 employment but commonly consumed by unemployed men, probably when hunting and living in the  
342 forest for long periods. This could also explain why so few birds are recorded during studies of  
343 bushmeat offtake in villages and markets, which often fail to account for social desirability bias or  
344 evasive responses to direct questioning (Nuno & St John 2015).

345 Bird hunting and consumption were predominantly dry season activities, but a peak  
346 occurred during the wet season in June. Although average monthly rainfall in June is high, in  
347 southern Cameroon there is a brief dry period at the beginning of the month (Stauffer & Smith  
348 2004). Thus, hunters may be exploiting improved weather conditions and maximising their efforts  
349 during this time. Most households also rely on locally farmed cassava *Manihot* sp., plantain *Musa x*  
350 *paradisiaca*, yam *Dioscorea* sp. and other crops for subsistence, and domesticated meat (chicken,  
351 pork) and fish are also consumed regularly. Bushmeat hunting is known to fluctuate in response to  
352 the seasonal availability of other food sources (Milner-Gulland EJ & Bennett 2003), and this might  
353 also explain the seasonal patterns in bird hunting and consumption seen here.

354 The timing of the peak in hunting activities is concerning, however, since longitudinal studies  
355 of both black-casqued and white-thighed hornbills in Cameroon show that breeding occurs in June  
356 (Stauffer and Smith 2004), when females are likely to be confined to nest cavities and males  
357 provisioning food. High levels of hunting during this stage of the reproductive cycle could therefore  
358 reduce fecundity and population viability through the selective killing of provisioning males or, if  
359 hunters are raiding nests, the loss of adult females and young.

360 Results from UCT questioning suggested that bird hunting prevalence was positively  
361 correlated with educational attainment, whereas direct questioning contradicted this finding and  
362 showed that consumption declined as educational attainment increased. We suggest this  
363 contradictory result is due to social desirability bias, and better educated individuals probably gave

364 evasive responses to direct questions. Thus, the anonymity provided by the UCT method revealed  
365 higher levels of hunting prevalence in this demographic. This is supported by similar work in  
366 Tanzania that also found hunting prevalence increased with educational attainment using the UCT  
367 method (Nuno et al. 2013). The link between education and hunting prevalence therefore requires  
368 further investigation. For example, do young men in education use hunting to pay for school fees  
369 and living costs, or to pay for non-essential items such as alcohol and cigarettes (Coad et al. 2010)?  
370 Or, are educated individuals generally wealthier and therefore able to afford a gun? Alternatively,  
371 can cultural reasons explain why educated individuals hunt birds, such as a reduced influence of  
372 cultural taboos? Answering these questions could prove valuable for socioeconomic initiatives aimed  
373 at decreasing hunting pressure through improved access to education and economic development.

374 Life-history and demographic data for affected species is sparse, making it difficult to assess  
375 hunting sustainability and population trends. Raptors were found at lower densities in hunted vs  
376 non-hunted forests in French Guiana (Thiollay 1984), and Asian forest hornbills have undergone  
377 widespread declines due to hunting pressure (Dasgupta & Hilaluddin 2012; Beastall et al. 2016). We  
378 therefore speculate that populations of large-bodied raptors and hornbills are also declining in our  
379 study area, and comparisons can be made with species that share similar life-histories. For example,  
380 population viability analysis for the Egyptian vulture *Neophron percnopterus*, which shares broad  
381 life-history traits with the raptors included in this study, showed that small reductions in survival  
382 rates of territorial and non-territorial birds (-0.015 and -0.008, respectively) significantly decreased  
383 time-to-extinction (Carrete et al. 2009). Based on density estimates from the literature, the ENP  
384 could support approximately 1702 palm-nut vultures (two pairs / km<sup>2</sup> and a juvenile population  
385 equal to 50% of the adult population; del Hoyo et al. 2016). Our estimates of c.84 individuals killed  
386 per annum (5% of the population) would therefore represent a reduction in survival of -0.05, five  
387 times greater than that needed to decrease Egyptian vulture time to extinction.

388 Crowned eagles (IUCN Near Threatened), which are also known to be hunted in the study  
389 area (Whytock & Morgan 2010) have a much slower generation time than palm-nut vultures,

390 maturing at c.5 years of age and requiring c.500 days to produce a single offspring, and are already  
391 considered rare in the ENP (Whytock & Morgan 2010). Therefore, even if only 20% ( $n = 2.4$   
392 individuals) of the approximately 12 'eagles' consumed per annum were crowned eagles this level of  
393 offtake would be sufficiently high to have a negative impact on populations. Black casqued and  
394 white-thighed hornbills have a more rapid generation time and are more abundant than large  
395 raptors in the ENP (Whytock & Morgan 2010). However, nest success rates for both species show  
396 high inter-annual variation linked to fruit availability, and within a 25 km<sup>2</sup> study area in Central  
397 Cameroon the number of active nests ranged from 0 to 38 per annum over a four-year period  
398 (Stauffer & Smith 2004). Alongside greater hunting pressure during the breeding season, these  
399 stochastic breeding cycles probably increase population sensitivity to hunting pressure.

400         Quantifying hunting sustainability in complex socio-ecological systems is challenging in  
401 general (Akçakaya et al. 2011; Van Vliet et al. 2015; Woodhouse et al. 2015), and inadequate  
402 assessments not only run the risk of overestimating sustainability, potentially resulting in  
403 overexploitation, but also risk harming the livelihoods and wellbeing of resource users if estimates  
404 are overly conservative (Woodhouse et al. 2015). Dynamic modeling techniques and agent-based  
405 models can offer novel insights by incorporating individual and spatial uncertainties in decision-  
406 making, for example from imperfect population monitoring (Van Vliet et al. 2015, Bunnefeld et al.  
407 2017). Given the likely vulnerability of affected birds based on their life histories (Owens & Bennett  
408 2000; Sæther & Bakke 2000; Trail 2007; Sreekar et al. 2015), the secretive nature of hunting  
409 activities, and because birds appear to be an important source of protein for unemployed men, we  
410 have avoided making a simplistic assessment of hunting sustainability here and recommend that  
411 future work firstly begins to monitor populations trends of affected species in the study area, and  
412 secondly investigates hunting sustainability using the suggested modeling techniques.

413

414 **Conclusion**



415 There is an urgent need to quantify hunting sustainability and to assess the population status of  
416 affected birds throughout their Central African range. Pending further assessment in other locations  
417 and in light of other threats such as habitat loss, we recommend that palm-nut vulture, black  
418 casqued hornbill and white-thighed hornbill are re-classified as Data Deficient (from Least Concern)  
419 by the International Union for the Conservation of Nature's Red List of Threatened Species™.

420 Biodiversity and livelihoods are threatened by unsustainable resource use in West and  
421 Central African forests. By providing respondents with anonymity and combining direct and indirect  
422 questioning techniques, our results reveal widespread, cryptic hunting of non-commercial taxa in  
423 Cameroon's forest communities.

424

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433

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550

551 **Table 1.** Parameter estimates (log odds, difference from the intercept) from the top generalised  
 552 linear mixed effects model explaining the probability of wild meat consumption in the past week.

Variable	Estimate	SE	Z	P
Intercept*	-0.58	0.81	-0.72	0.47
Employment (employed)	-2.39	1.03	-2.33	0.02
Employment (temporary)	-0.06	0.37	-0.15	0.88
Education (secondary+)	-1.01	0.26	-3.86	< 0.001
Education (no formal)	-0.30	0.26	-1.14	0.26
Gender (female)	-0.74	0.16	-4.55	< 0.001
Month (March)	-1.20	0.29	-4.14	< 0.001
Month (April)	-0.84	0.61	-1.37	0.17
Month (May)	-2.57	0.59	-4.38	< 0.001
Month (June)	0.35	1.06	0.33	0.74
Taxa (mammal)	1.42	1.04	1.37	0.17
Age	-0.01	0.01	-0.88	0.38
Education (secondary+):taxa (mammal)	0.81	0.31	2.64	0.008
Education (no formal): taxa (mammal)	-0.52	0.33	-1.59	0.11
Taxa (mammal):age	0.01	0.01	1.70	0.09
Taxa (mammal):month (March)	2.00	0.35	5.79	< 0.001
Taxa (mammal):month (April)	0.91	0.29	3.18	0.001
Taxa (mammal):month (May)	1.40	0.31	4.47	< 0.001
Taxa (mammal):month (June)	0.56	0.52	1.09	0.28
Taxa (mammal):employment (employed)	0.83	1.07	0.78	0.44
Taxa (mammal):employment (temporary)	-0.41	0.43	-0.97	0.33
Taxa (mammal):gender (female)	0.36	0.20	1.82	0.07

553 \*Intercept: February bird consumption estimate for male educated to primary level and unemployed  
 554 in the past 12 months  
 555

556 **Figure 1.** Proposed Ebo National Park (shaded, inset) and departments (dashed lines, inset) in  
557 Littoral Region, Cameroon. Locations of villages surveyed are not shown for ethical reasons (St. John  
558 et al. 2016).

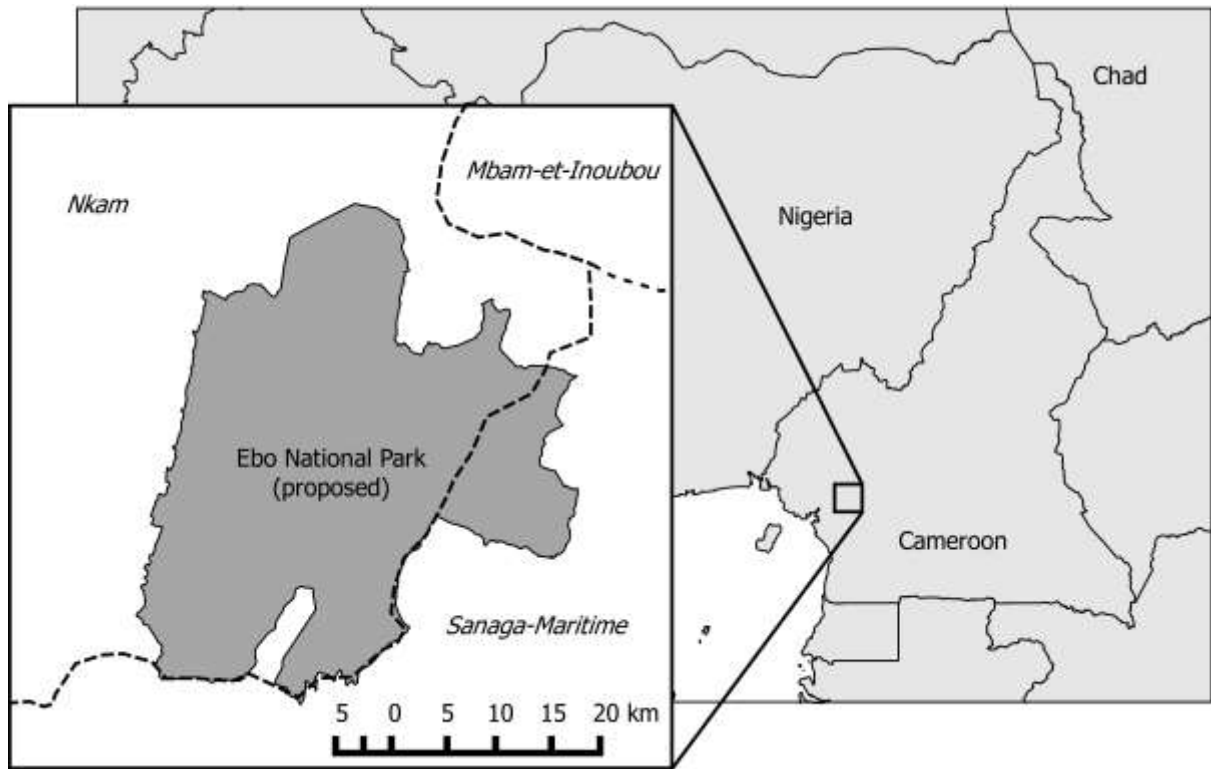
559 **Figure 2.** Education level and the estimated prevalence (filled circle  $\pm 95\%$  CI) of bird hunting during  
560 the dry season. The estimated baseline prevalence (gray circle  $\pm 95\%$  CI) for the population is also  
561 shown.

562 **Figure 3.** Effects of season, socioeconomic and demographic factors on the probability of consuming  
563 a wild bird or mammal in the past week estimated from the generalised linear mixed effects model  
564 for bird consumption. Estimates and confidence intervals have been back-transformed to the  
565 probability scale, and summary statistics for the model are given in Table 1. Densities of raw data  
566 points for yes (1) or no (0) answers are also shown.

567 **Figure 4.** Estimated number of individuals consumed (assuming 50 g of meat per meal) per month  
568 for each species or species group (conditional modes of the intercept  $\pm 95\%$  CI from a generalised  
569 linear mixed effects model for bird consumption) by unemployed males educated to primary level ( $n$   
570 = 240 respondents). Non-focal fixed effects were set to their median value for continuous variables  
571 or most common level for categorical variables. Dashed gray lines show the estimated mean  
572 monthly offtake. The y-axis is on a log-scale.

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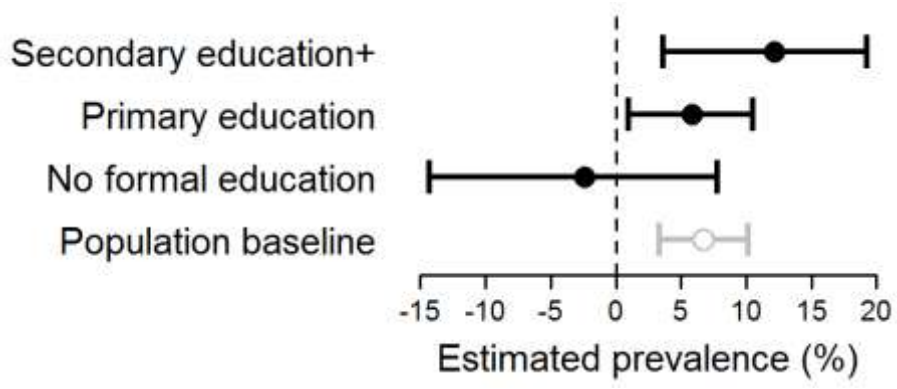


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Figure 1

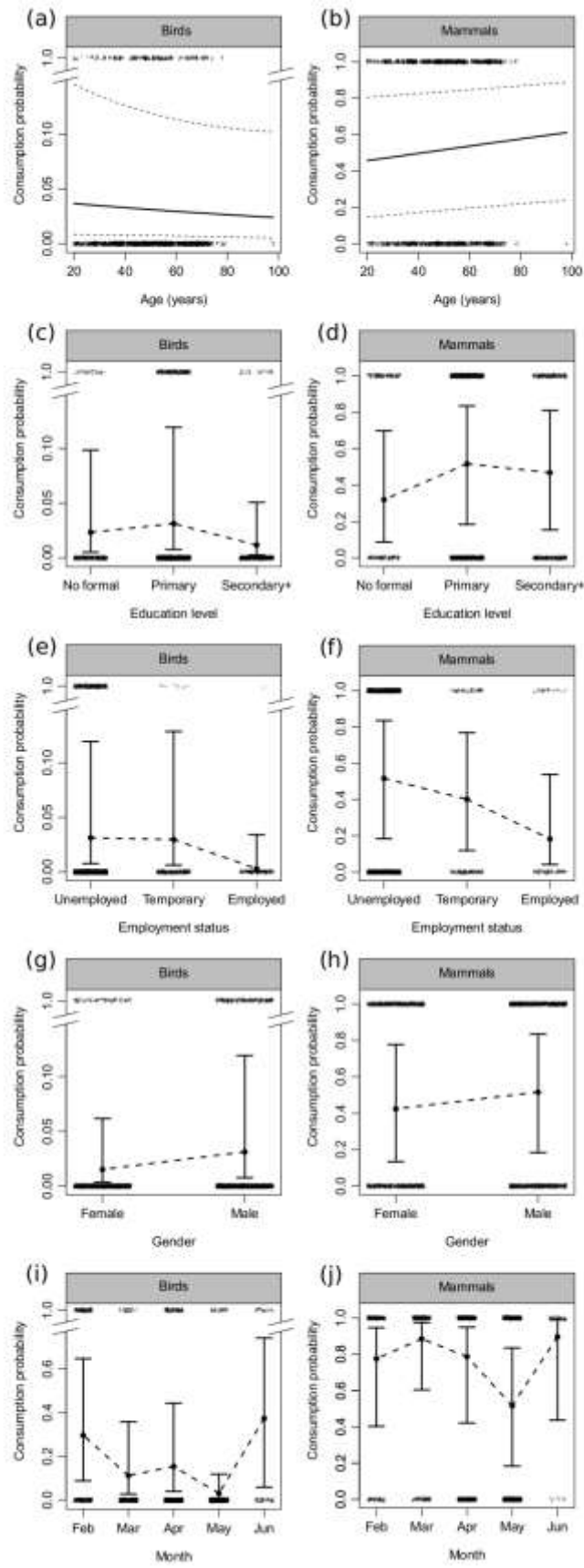


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Figure 2

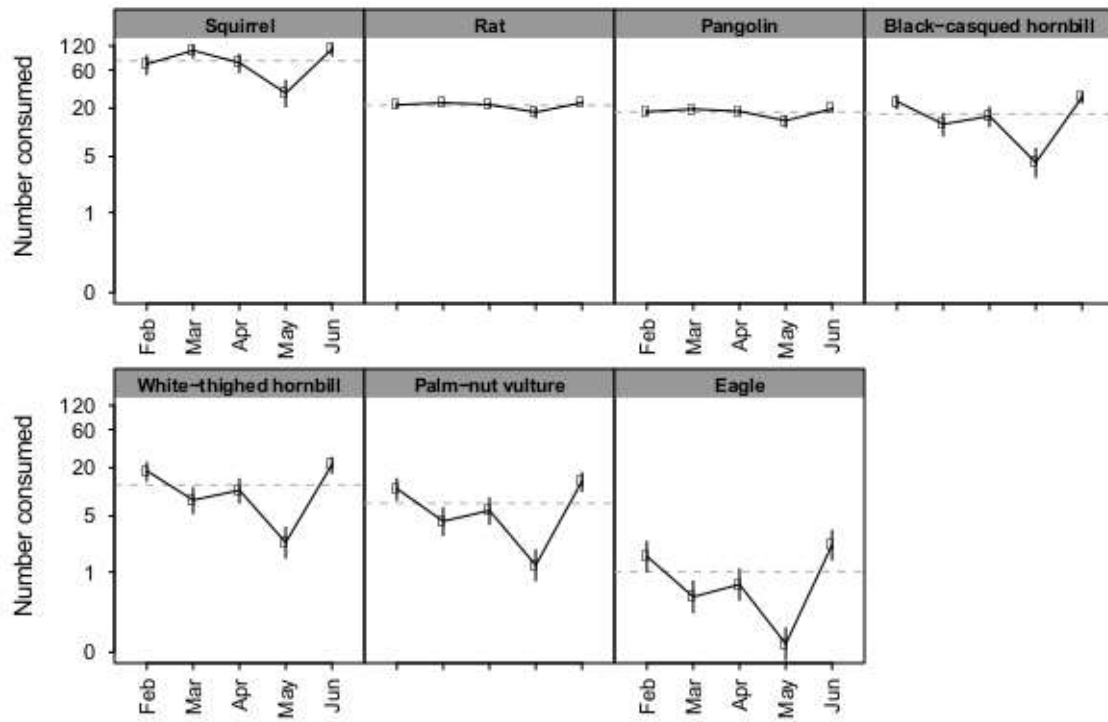


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Figure 3



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Figure 4