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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 km². 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 km²) 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 ≥ 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 ± 7.7 SE, and the mean number of interviews per month was 135
187 ± 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 ΔAICc 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). 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 / km² 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 km² 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

434

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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

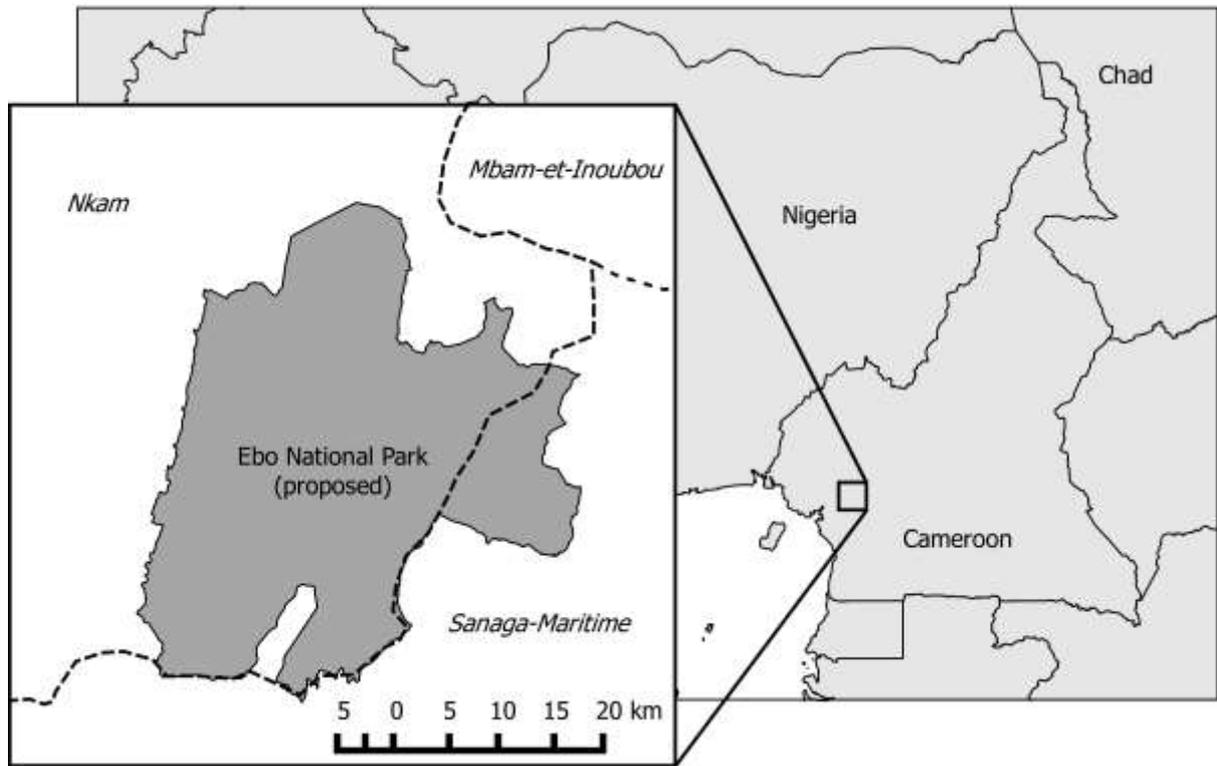
556 **Figure 1.** Proposed Ebo National Park (shaded, inset) and departments (dashed lines, inset) in
557 Littoral Region, Cameroon. Locations of villages surveyed are not shown for ethical reasons (St. John
558 et al. 2016).

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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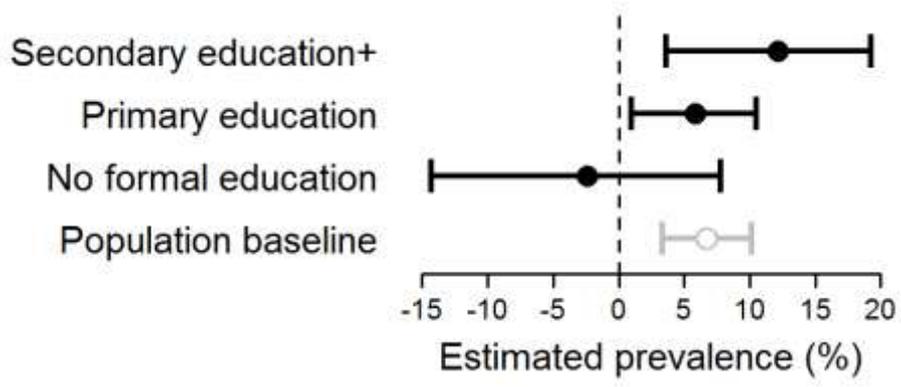


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Figure 1

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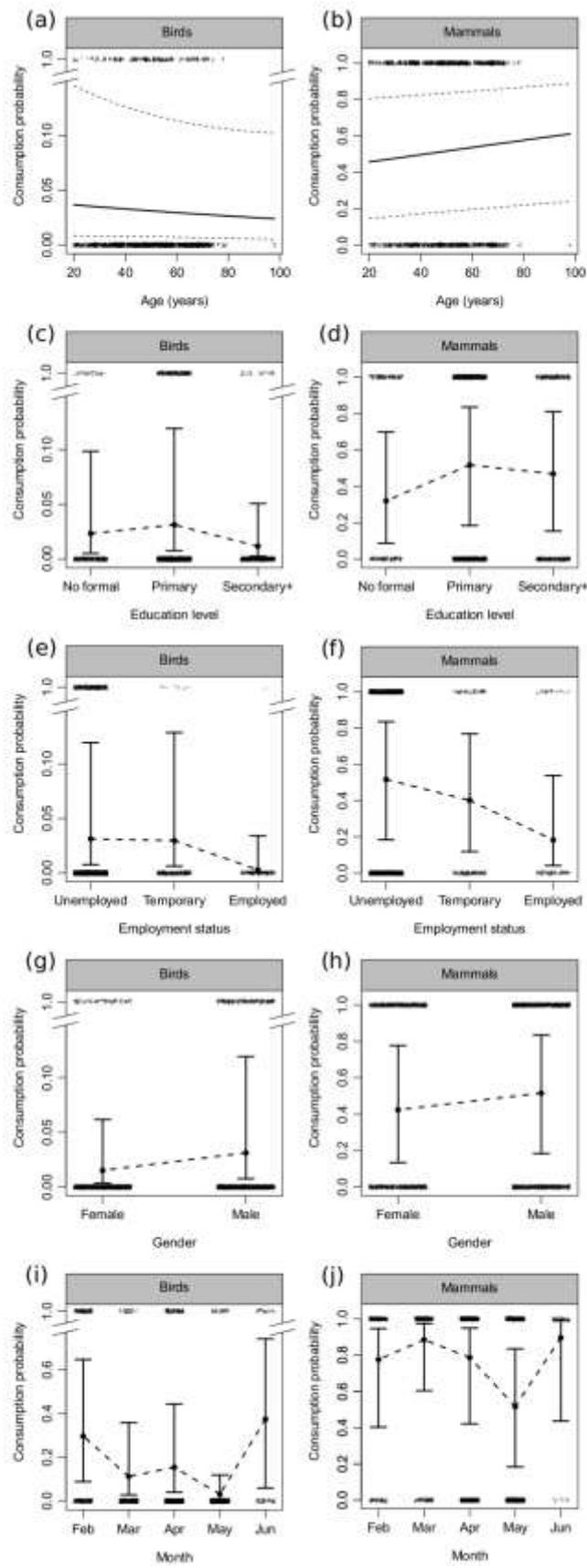


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Figure 2

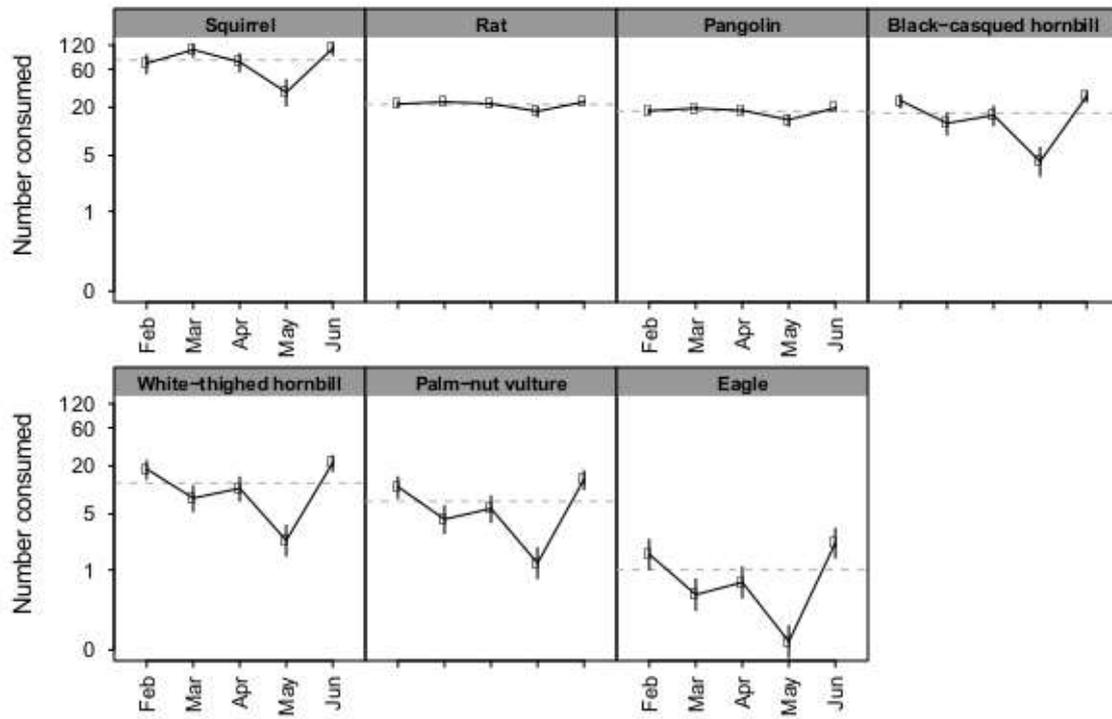


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Figure 3



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Figure 4