1	Sustainable wildlife extraction and the impacts of socio-economic change among the
2	Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru.
3	
4	Maire Kirkland ^{a,b,c*} , Cristina Eisenberg ^d , Andy Bicerra ^a , Richard E. Bodmer ^{a,e} , Pedro
5	Mayor ^{a,f} and Jan C. Axmacher ^c
6	
7	^a Fund Amazonia, Calle Malecón Tarapacá N° 332, Iquitos, Peru.
8	^b Durham University, Stockton Road, Durham DH1 3LE, UK.
9	^c UCL Geography, University College London, Gower St, London WC1E 6BT, UK.
10	^d Earthwatch, 114 Western Avenue, Boston, MA 02134, USA.
11	^e University of Kent, Canterbury CT2 7NZ, UK.
12	^f Universitat Autònoma de Barcelona, Barcelona, 08193, Spain.
13	
14	*Corresponding author (phone: 00447903669271, email: maire.kirkland@durham.ac.uk,
15	Department of Biosciences, Durham University.)
16	
17	emails: maire.kirkland@durham.ac.uk, ceisenberg@earthwatch.org,
18	andybicerra@gmail.com, r.bodmer@kent.ac.uk, mayorpedro@hotmail.com,
19	j.axmacher@ucl.ac.uk
20	
21	Word count: 5679
22	
23	
24	
25	

26 Sustainable wildlife extraction and the impacts of socio-economic change among the

27 Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru.

28

29 Abstract

30

31 Throughout the tropics, hunting and fishing are critical livelihood activities for many 32 Indigenous peoples. However, these practices may not be sustainable following recent 33 socio-economic changes in Indigenous populations. Aiming to understand how human 34 population growth and increased market integration affect hunting and fishing patterns, 35 we conducted semi-structured interviews in five Kukama-Kukamilla communities living 36 along the boundary of the Pacaya-Samiria National Reserve, in the Peruvian Amazon. 37 Extrapolated annual harvest rates of fish and game species by these communities 38 amounted to 1,740 t and 4,275 individuals (67 t), respectively. At least 23 fish and 27 39 game species were harvested. We found a positive correlation between village size and 40 annual total community-level harvest rates of fish and a negative relationship between 41 market exposure and mean per-capita harvest rates of fish. Catch-per-unit-effort 42 (CPUE) analyses indicated local depletion of fish populations around larger, more 43 commercial communities. CPUE of fish was lower in more commercial communities 44 and fishermen from the largest village travelled farther into the reserve, where CPUE 45 was higher. We found no effect of village size or market exposure on harvest rates or 46 CPUE of game species. However, larger, more commercial communities targeted larger, 47 economically valuable species. This study provides evidence that human population 48 growth and market-driven hunting and fishing pose a growing threat to wildlife and 49 Indigenous livelihoods through increased harvest rates and selective harvesting of 50 vulnerable species.

52 *Keywords:* Sustainability; Hunting; Fishing; Protected area; Amazon.

53

54 Introduction

55

56 In tropical forests, hunting and fishing are crucial to the livelihoods of Indigenous 57 peoples as a source of protein and income (East et al., 2005). Unfortunately, a growing 58 number of studies suggest current harvests of a variety of species exceed sustainable 59 levels, causing widespread population declines and local extinctions (Abernethy et al., 60 2013; Castello et al., 2014; Morcatty & Valsecchi, 2015; Parry & Peres, 2015). As a 61 result, the sustainability of hunting and fishing has become the subject of considerable 62 concern among ecologists, anthropologists, protected area managers and 63 conservationists alike. This has sparked a debate surrounding the presence of 64 Indigenous peoples in protected areas, between those who view them as a direct threat 65 to biodiversity and those who view them as conservation allies (da Silva et al., 2005; 66 Ohl-Schacherer et al., 2007). In-depth monitoring of hunting and fishing is a key 67 prerequisite to promoting the sustainable use of natural resources, avoiding extinctions 68 of important species while preserving the rights of Indigenous peoples to land, 69 traditions, and culture.

70

The decreasing sustainability of hunting and fishing practices has been attributed in part to the rapid growth in Indigenous populations and their integration into the market economy. These trends have triggered powerful socio-economic changes, leading to an increasing demand for wildlife products from both the rural and urban populations and a growing economic incentive to hunt and fish commercially

76 (McSweeney & Jockisch, 2007; Ohl-Schacherer et al., 2007; Suarez et al., 2009; Fa et 77 al., 2015). Simultaneously, improved technologies and transportation have enhanced the 78 capacity of a growing number of hunters and fishermen to capture prey, including in 79 previously inaccessible areas (Wilkie et al., 2000; Godoy et al., 2010; Foerster et al., 80 2012). Yet, empirical studies have revealed mixed and even positive effects of socio-81 economic development on wildlife harvesting (Lu, 2007). For example, opportunities 82 for permanent and well-paid jobs combined with a preference among wealthier 83 households for alternative protein sources like store-purchased meat can lead to a 84 reduction in wildlife harvesting (Wilkie & Godoy, 2001; Gray et al., 2015; Vasco & 85 Sirén, 2016). Understanding the complex interactions between socio-economic factors 86 and extractive activities in a variety of social, cultural, and natural contexts remains 87 imperative, especially given the need to alleviate poverty among Indigenous peoples. 88

89 In the Peruvian Amazon, hunting and fishing constitute integral components of 90 the Kukama-Kukamilla culture. This Indigenous group harvests a large variety of 91 natural resources from their surrounding areas that include the Pacaya-Samiria National 92 Reserve (PSNR). In the past, a strict protectionist system in this reserve provoked a 93 backlash of rampant poaching and over-exploitation by the local people (Bodmer et al., 94 2008). In the late 1990s, a new reserve administration adopted a co-management 95 approach, permitting low levels of hunting and fishing by the local people. Since then, 96 populations of key species have been increasing in the reserve, including threatened 97 species such as the woolly monkey Lagothrix spp., lowland tapir Tapirus terrestris and 98 paiche Arapaima gigas (Bodmer & Puertas, 2007). However, like many other 99 Amazonian communities, the Kukama-Kukamilla are undergoing rapid socio-economic 100 changes that could once again increase pressure on wildlife.

102 In this study, we aimed to explore how socio-economic factors influence the 103 hunting and fishing patterns of the Kukama-Kukamilla people. The results of this study 104 provide important insights into the factors that underpin sustainable resource use, 105 specifically the risk of human population growth and market-driven hunting and fishing 106 brought about by rural development. Previous studies have generally explored the 107 effects of socio-economic conditions on wildlife harvesting between households. 108 However, because households within a community harvest wildlife from a communal 109 catchment area, we explored the combined impacts of wildlife harvesting by the 110 community as a whole. Through the use of semi-structured interviews, we tested the 111 hypothesis that larger communities with greater access to the economic market exert 112 higher pressure on wildlife and target more commercially valuable species. These 113 communities are expected to be affected by higher levels of wildlife depletion, with 114 preferred species disappearing near villages, triggering shifts in harvested species 115 spectra. 116 117 Study area

118

This study was carried out in the PSNR, which covers an area of 2,080,000 ha in the Department of Loreto, in the north-eastern Peruvian Amazon. It is bordered by two tributaries of the Amazon River, the Ucayali and Marañón rivers, and encompasses the two major drainage basins of the Pacaya and Samiria rivers. The reserve is characterised by massive hydrological fluctuations that occur between the high-water (October to May) and low-water (June to September) seasons (Kvist et al., 2001).

126	The majority of inhabitants are descendants of the Tupi-Guarani speaking
127	Kukama-Kukamilla people and more recent immigrants of Caucasian and Indigenous
128	origin (Gow, 2007). Their main livelihood activity is fishing, which is most productive
129	during the low-water season, when fish become trapped in the shrinking water bodies.
130	Nonetheless, migrations of fish feeding on fallen fruit in the várzeas (white-water
131	flooded forests) make some fisheries productive during the high-water season (Kvist et
132	al., 2001). The Kukama-Kukamilla also engage in opportunistic hunting, primarily
133	during the high-water season, when the terrestrial fauna is concentrated on the non-
134	inundated restingas (levees) (Bodmer et al., 1998).
135	
136	Approximately 100,000 people live in over 200 communities along the boundary
137	of the PSNR (INRENA, 2009). We selected five Kukama-Kukamilla villages located at
138	the mouth of the Samiria River, which were divided into two distinct areas: a) San
139	Martín de Tipishca, Nuevo Arica and Bolivar lie on the shores of the Tipishca Lake; and
140	b) San José de Samiria and Leoncio Prado are located along the Marañón River (Fig. 1).
141	These villages ranged from 40 to 120 households (Table 1), and differed in their
142	exposure to the market economy. The communities of the Marañón River supply
143	produce to the urban markets of Loreto by selling to freezer vessels or directly to market
144	vendors.
145	
146	Methods
147	
148	Data collection
149	
150	We conducted 122 semi-structured interviews, which accounted for 34.9% of

151 households within the study area, between June-August 2013 (Table 1). The use of 152 semi-structured interviews was the preferred data collection method, as they allow 153 emphasis on specific topics depending on the interviewees' knowledge and experience 154 (Rubin & Rubin, 2005). Recall bias was expected to be minimal, as quantitative 155 information asked was simple and activities are regular and highly seasonal (Golden et 156 al., 2013). All households were found to be dependent on hunting and/or fishing, so we 157 adopted a convenience sampling approach, selecting the most accessible households 158 (Patton, 2002). We targeted male heads of households for interviews, but in some cases 159 interviewed women instead, either because they too participated in hunting or fishing, or 160 more often they had acquired detailed information about harvests through cooking. We 161 obtained prior informed consent from participants before conducting interviews.

162

163 The social sensitivity of the topic being explored may have created some bias in 164 the data resulting from the under-representation of harvests. Where possible, we used 165 participant observation to verify interview responses. We informed interviewees that no 166 information gathered would be used against them and that survey information would be 167 anonymised.

168

169 Data analysis

170

We obtained household harvest rates of fish by asking fishermen to state the mean total biomass of fish caught per day, during high- and low-water seasons separately. This was extrapolated to annual harvest rates by multiplying each estimate of mean daily yield for each season by 182.5 (6 months). A limitation of using interviews to collect harvest data was that fishermen were unable to state the quantity of each species harvested, because

176 they measure the weight of the entire catch. We therefore recorded the percentage of 177 households that harvest each species, using these data as proxies for relative harvest 178 rates. We obtained annual household harvest rates of game species by asking hunters to 179 state the mean number of wild animals hunted per year for each species, as hunting is 180 less frequent than fishing. This was converted to biomass using body weight data 181 reported by Peres and Dolman (2000), Ohl-Schacherer et al. (2007), Cardoso et al. 182 (2012), and Mayor et al. (2015). We calculated per-capita harvest rates, assuming an 183 average of six individuals per household. We determined total community-level harvest 184 rates of fish by multiplying mean household harvest rates by the number of households 185 in each community, and in the case of game species, by the percentage of households 186 that engage in hunting.

187

188 We used household harvest rates to estimate catch-per-unit-effort (CPUE). The 189 assumption behind CPUE as an indicator of sustainability is that hunters and fishermen 190 must increase their efforts in areas with depleted populations to achieve the required 191 meat and fish return rates. A difference in CPUE is assumed to reflect a difference in 192 actual prey density or abundance (Rist et al., 2010). We calculated CPUE of fish as Y/H 193 and CPUE of game species as B/D, where Y is the total daily yield of fish harvested; H 194 is the number of hours a day fishermen leave their nets in the water (the most common 195 method); B is the total biomass of games species hunted annually; and D is the number 196 of days a year hunters are active. We averaged across households to obtain community-197 level CPUE estimates.

198

We calculated the distance travelled on hunting and fishing trips using reports ofaverage time travelled. Based on information given by a local informant, we estimated

201 that 6 km were travelled in 1 hour in *peque peque* (motorized canoe) and 4 km on foot. 202 Since hunters use watercourses to navigate to hunting sites and limit their activities to 203 within 2 km into the forest from the river's edge, distance travelled was multiplied by 204 four to obtain the size of the total catchment area (Begazo & Bodmer, 1998). The 205 corresponding catchment area was drawn around the channels and lakes of the Samiria 206 and Marañón rivers and divided into zones of low, medium, and heavy exploitation, 207 using the maximum distances travelled by the top 25% and 50% percentiles as the 208 thresholds (Fig. 2). Given our project's social science dimension and use of interviews, 209 we determined that this measure of relative exploitation was appropriate (Brodizio & 210 Chowdhury, 2010; Hawken & Munch, 2012). We used Welch's analysis of variance 211 and the Kruskal-Wallis H test to compare distance travelled on hunting and fishing trips 212 between communities. The Pearson's rank correlation coefficient allowed us to examine 213 the relationship between CPUE and distance travelled as an indication of local resource 214 depletion (Fa et al. 2006; Laurance et al. 2006).

215

216 We used multiple linear regressions to investigate the effects of socio-economic 217 variables on CPUE and harvest rates. We included village size as a continuous variable 218 and market exposure as a categorical variable in all models, using season as an 219 additional categorical variable in the analyses of fishing data. The response variables 220 were log-transformed to account for non-normal distributions. We estimated the 221 significance of variables by dropping them from the full model and using likelihood 222 ratio tests to compare nested models. We examined variations in the species 223 compositions of harvests, termed the 'harvest profile', using Principal Components 224 Analysis (PCA). Results were considered significant for P < 0.05. Statistical analyses 225 were undertaken in R version 3.3.1 (R Core Team, 2016).

227 Results

228

229 All households in the study area fished daily throughout the year. In 57% of households, 230 fishing was supplemented with hunting. 77% of hunters were active less than 10 days a 231 year, and only one hunted as often as 18 days a year. The total biomass of wildlife 232 harvested annually by the five communities was \sim 1,807 t (Table 1). The majority of 233 fishermen (96%) reported travelling in *peque peque* for no more than 6 hours, whereas 234 39% of hunters undertook trips of several days, travelling over 6 hours to reach remote 235 *restingas* inside the reserve. The mean distance travelled by fishermen and hunters was 236 11.2 (\pm 4.1) km and 44.0 (\pm 11.1) km, respectively. The distance travelled on hunting 237 trips did not differ between communities ($H_{(4)} = 5.70$, P = 0.22), but fishermen from 238 Nuevo Arica and San Martín de Tipishca travelled farther than fishermen from other 239 villages (*Welch's* $F_{(4,29.67)} = 18.21$, P < 0.001). The combined hunting and fishing catchment area for all communities covered ~576 km² (Fig. 2). There was a positive 240 241 correlation between distance travelled into the reserve and CPUE of fish during the low-242 water season (Pearson $r_{s(120)} = 0.22$, P = 0.017), but not the high-water season (Pearson 243 $r_{s(120)} = 0.17$, P = 0.07). No significant correlation existed between distance travelled and 244 CPUE of game species (Pearson $r_{s(69)} = 0.14$, P = 0.24). 245

The communities of the Samiria basin collectively harvested 1,740 t of fish annually
(96.3% of biomass extracted), comprising 23 fish species (Table 2). The most widely
caught species was *Prochilodus nigricans*, a species of both commercial and subsistence
importance. There was substantial variation in harvest profiles between communities
(Fig. 3). In San José de Samiria and Leoncio Prado, fishermen harvested a large

proportion of small, commercial species such as *Leporinus* spp., as well as larger species like *Hoplias malabaricus*. In San José de Samiria, smaller, less economically valuable species like *Oxydoras niger* and *Leiarius marmoratus* also made up a significant proportion of their catch. The communities of the Tipishca Lake depended on the most abundant species, including *Pterygoplichthys pardalis*, *Pygocentrus* spp. and *Serrasalmus* spp. We found evidence that the paiche, a species of conservation concern, was also caught.

258

259 The reported total annual harvest of game species in the study area was ~4,275 260 individuals, equating to ~67 t (3.7% of biomass extracted) and comprising 27 species 261 (Table 3). Mammals were the most frequently extracted group, making up 74.0% of 262 hunted biomass and 56.0% of all hunted individuals, followed by reptiles (23.1%; 263 19.1%) and birds (2.9%; 24.9%). The majority of biomass harvested came from large-264 bodied animals, mainly the white-lipped peccary (Tayassu pecari), lowland tapir, and 265 black caiman Melanosuchus niger. The white-lipped peccary, paca Cuniculus paca and 266 brown agouti Dasyprocta variegata were the most frequently hunted in terms of number 267 of individuals. The Amazonian manatee *Trichechus inunguis*, which is strictly 268 protected, was hunted occasionally. As with fish harvests, harvest profiles of game 269 species varied substantially between communities (Fig. 4). In San José de Samiria and 270 San Martín de Tipishca, hunters harvested a larger proportion of large-bodied species, 271 such as the lowland tapir, the South American river turtle *Podocnemis expansa* and the 272 white-lipped peccary, whereas the other communities harvested a larger proportion of 273 small primates and wetland birds.

274

275

The multiple linear regressions revealed a significant positive relationship

276	between village size and annual community-level harvest rates of fish (Table 4, Fig. 5).
277	However, village size had no effect on mean per-capita harvest rates ($F = 0.33$, $P =$
278	0.59) or CPUE ($F = 0.96$, $P = 0.37$) of fish. In contrast, there was no effect of market
279	exposure on community-level harvest rates of fish ($F = 4.60, P = 0.08$), but commercial
280	communities had significantly lower mean per-capita harvest rates and CPUE of fish
281	(Table 4, Fig. 6-7). As expected, season had a significant effect on harvest rates and
282	CPUE of fish, both of which were higher in the low-water season (Table 4). Neither
283	market exposure nor village size had a significant effect on harvest rates or CPUE of
284	game species (all $P > 0.31$).

286 **Discussion**

287

288 Our study adds to the growing body of research that suggests that socio-economic 289 factors influence wildlife harvesting by Indigenous peoples (Smith & Wishnie, 2000; 290 Lu, 2007; Godoy et al., 2010). Specifically, the patterns of hunting and fishing by the 291 Kukama-Kukamilla people of the PSNR reveal the potential threat of increased market 292 integration and a rising human population. The data presented in this study include a 293 number of potential sources of variation that we did not control for, including 294 environmental variables such as habitat quality, which may have limited the statistical 295 power of the analyses. Furthermore, the small sample size of only five communities 296 means caution must be taken when interpreting the results of the significance tests. 297 However, because data points represent aggregates of household-level data, they reflect 298 many more underlying observations, and we believe this allows us to make reliable 299 inferences.

300

301 We discovered evidence that increased market exposure leads to resource 302 depletion, reflected in a lower CPUE of fish in commercial communities. A reduction in 303 fish populations as a result of over-fishing may have reduced the profitability of fishing 304 and limited commercial fishing activity, which would explain why fishermen in 305 commercial communities had lower mean per-capita harvest rates (Vasco & Sirén, 306 2016). Nevertheless, the net pressure that commercial fishing puts on depleted resources 307 is likely greater than the pressure exerted by non-commercial communities on relatively 308 un-depleted fish stocks. In San José de Samiria and Leoncio Prado, fishermen targeted 309 small, economically valuable species, indicating possible over-exploitation of larger 310 species. This trend is observed in the nearby markets of Iquitos, where the sale of 311 cheaper, smaller and faster-growing species has risen since the 1980s and the sale of 312 larger species has declined (Garcia et al., 2008; Atwood et al., 2015). The large 313 proportion of less economically valuable species in harvests from San José de Samiria 314 could reflect an increasing reliance on these species for subsistence.

315

316 As expected, larger communities exerted greater pressure on fish resources 317 through increased harvest rates, because there is both more people to feed and a greater 318 number of fishermen. We therefore expected to see similar signs of resource depletion 319 in these communities. Nonetheless, community size had no significant effect on CPUE 320 of fish. However, fishermen from San Martín de Tipishca, the largest village, together 321 with those from Nuevo Arica, travelled farther on fishing trips than those from 322 neighbouring communities, and during the low-water season CPUE was higher farther 323 into the reserve. This is consistent with the paradigm that Neotropical people are 324 central-place foragers, travelling greater distances in search of preferred prey species as 325 wildlife populations become locally depleted (Levi et al., 2009; 2011). Thus, fishing in

previously un-exploited sites inside the PSNR could be masking resource depletion in
the Tipishca Lake. Fishermen from San Martín de Tipishca also harvested small,
abundant fish species, which may be able to sustain the larger human population.

330 We found no clear effect of village size or market exposure on harvest rates or 331 CPUE of game species. This implies that people in larger, commercial villages have 332 been able to shift to alternative sources of protein, such as fish or livestock, to meet 333 subsistence and commercial needs. The strong presence of preferred species in harvest 334 profiles suggests that wild meat harvests in the PSNR are currently supplied by a 335 relatively un-depleted source. In San José de Samiria and San Martín de Tipishca, 336 hunters harvested large-bodied prey species, including ungulates, large primates and 337 reptiles. Encounter rates of these species in the forest are relatively low due to naturally 338 low population densities, so hunters are likely targeting them for their greater meat 339 harvests, as occurs in other Amazonian communities (Peres & Lake, 2003; Zapata-Ríos 340 et al., 2009; Espinosa et al., 2014; Sirén & Wilkie, 2016). The current hunting patterns 341 of the Kukama-Kukamilla people may be indicative of a source-sink dynamic, with 342 immigration of game species from the un-hunted core zone of the reserve sustaining 343 harvests in the catchment area (Navaro et al., 2000; Ohl-Schacherer et al., 2007).

344

Nevertheless, large-bodied game species are particularly vulnerable to overexploitation due to slow reproductive rates (Mayor et al., 2017). The continued harvest of vulnerable species by larger, commercial communities will likely cause significant population declines in the PSNR and a shift in prey selection toward a broader range of smaller, less-preferred species, following the general trend observed throughout the Amazon (Naranjo & Bodmer, 2007; Peres & Palacios, 2007; Constantino, 2016). The

region has also been experiencing more extreme droughts and seasonal flooding in the
last few decades, which could exacerbate the impacts of unsustainable wildlife
extraction by limiting resources for wildlife and causing direct mortality of animals
(Bodmer et al., 2017). The recent sharp decline in populations of the white-lipped
peccary throughout its range, for which non-anthropogenic impacts are suspected, will
put further pressure on alternative and more vulnerable prey species (Fragoso, 2004;
Richard-Hansen et al., 2013; Mayor et al., 2015).

358

359 Overall, our results indicate that the forests of the PSNR are able to provide 360 important food supplements for the Kukama-Kukamilla people. However, hunting and 361 fishing in some villages appears to be approaching critical thresholds, threatening the 362 natural capital of the reserve. Around the world, the combination of human population 363 growth and increased market integration of Indigenous peoples is linked to a downward 364 spiral of local species extinctions and a diminishing supply of crucial protein and 365 income. In this context, the sustainable management of natural resources represents a 366 crucial opportunity for biodiversity conservation where protected areas and Indigenous 367 territories overlap (Zimmerman et al., 2001). Development professionals, protected area 368 managers, and conservationists need to help maintain low hunting and fishing pressure 369 by diversifying and enhancing existing livelihood strategies, thereby reducing poverty 370 in rural communities and conserving vulnerable species (Bodmer & Lozano, 2001; 371 Bassett, 2005; Gandiwa, 2011). Community-based management is needed to monitor 372 the impacts of socio-economic and climatic change, and to ensure the long-term 373 sustainable use of forest species, both inside and outside protected areas. 374

375 Author contributions

377	REB and MK designed the data collection methods and REB provided logistical support
378	in the field. MK collected and analysed the data and wrote the first draft of the
379	manuscript. JCA, MK, CE, REB and PM edited the manuscript to produce the final
380	draft. AB produced the maps.
381	
382	Acknowledgements
383	
384	We are indebted to the incredible support provided by the communities of the Pacaya-
385	Samiria National Reserve, who participated in data collection and without whom this
386	project would not have been possible. We thank Teddy Urashima and Pool Erazo
387	Arevalo for field assistance, Pablo Puertas for his help and advice and Hannah Kirkland
388	for proof reading. We also thank Fund Amazonia, Wildlife Conservation Society,
389	Earthwatch Institute, and Operation Wallacea for assistance during fieldwork and
390	financial support. Finally, many thanks to the Peruvian Protected Area Service –
391	SERNANP – for providing authorization for and coordination of fieldwork.
392	
393	References
394	
395	Abernethy, K., Coad, L., Taylor, G., Lee, M. & Maisels, F. (2013) Extent and
396	ecological consequences of hunting in Central African rainforests in the 21st
397	century. Philosophical Transactions of the Royal Society B, 368, doi:
398	10.1098/rstb.2012.0303.
399	Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays,
400	G.C., Fourqurean, J.W. & Macreadie, P.I. (2015) Predators help protect carbon

- 401 stocks in blue carbon ecosystem. *Nature Climate Change*, 5(12), 1038-1045.
- 402 Bassett, T.J. (2005) Card-carrying hunters, rural poverty, and wildlife decline in
- 403 northern Côte d'Ivoire. *Geography Journal*, 171, 24-35.
- 404 Begazo, A.J. & Bodmer, R.E. (1998) Use and conservation of Cracidae (Aves:
- 405 Galliformes) in the Peruvian Amazon. *Oryx*, 32, 301-309.
- 406 Bodmer, R.E. & Lozano, E.P. (2001) Rural development and sustainable wildlife use in
- 407 the tropics. *Conservation Biology*, 15, 1163-1170.
- 408 Bodmer, R.E., Mayor, P., Antunez, M., Chota, K., Fang, T., Puertas, P., Pittet, M.,
- 409 Kirkland, M., Walkey, M., Rios, C., Pérez-Peña, P., Henderson, P., Bodmer, W.,
- 410 Bicerra, A., Zegarra, J. and Docherty, E. (2017) Major shifts in Amazon wildlife
- 411 populations from recent climatic intensification. *Conservation Biology*, doi:
- 412 10.1111/cobi.12993.
- 413 Bodmer, R.E & Puertas, P.E. (2007) Impacts of displacement in the Pacaya-Samiria
- 414 National Reserve, Peru. In Protected Areas and Human Displacement: A
- 415 *Conservation Perspective* (eds K.H. Redford & E. Fearn), pp. 29-33. WCS
- 416 Working Papers: N° 29, WCS.
- 417 Bodmer, R.E., Puertas, P.E. & Fang, T.G. (2008) Co-managing wildlife in the Amazon
- 418 and the salvation of the Pacaya-Samiria National Reserve in Peru. In *Wildlife and*
- 419 Society. The Science of Human Dimensions (eds M. Manfredo, J. Vaske, P. Brown,
- 420 D. Decker & E. Duke), pp. 104-116. Island Pess, Washington DC, USA.
- 421 Bodmer, R.E., Puertas, P.E., Garcia, J.E., Diaz, D.R. & Reyes, C. (1998) Game animals,
- 422 palms and people of the flooded forests: management considerations for the
- 423 Pacaya-Samiria National Reserve, Peru. Advances in Economic Botany, 13, 217-
- 424 232.
- 425 Brodizio, E.S. & Chowdhury, R.R. (2010) Spatio-temporal methodologies in

- 426 environmental anthropology: geographic Information Systems, Remote Sensing,
- 427 landscape changes, and local knowledge. In *Environmental Social Sciences:*
- 428 Methods and Research Design (eds I. Vaccaro, E.A. Smith & S. Aswani), pp. 266-
- 429 289. Cambridge University Press, Cambridge, UK.
- 430 Cardoso, A.M.C., de Souza, A.J.S., Menezes, R.C., Pereira, W.L.A. & Tortelly, R.
- 431 (2012) Gastric lesions in free-ranging black caimans (*Melanosuchus niger*)
- 432 associated with *Brevimulticacum* species. *Veterinary Pathology*, 50, 582-584.
- 433 Castello, L., Arantes, C.C., McGrath, D.M., Stewart, D.J. & de Sousa, F.S. (2014)
- 434 Understanding fishing-induced extinctions in the Amazon. *Aquatic Conservation:*
- 435 *Marine and Freshwater Ecosystems*, 25(5), 587-589, doi: 10.1002/aqc.2491.
- 436 Constantino, P. (2016) Deforestation and hunting effects on wildlife across Amazonian
- 437 indigenous lands. *Ecology and Society* 21(2), 3, doi: 10.5751/ES-08323-210203.
- 438 East, T., Kümpel, N.F., Milner-Gulland, E.J. & Rowcliffe, J.M. (2005) Determinants of
- 439 urban bushmeat consumption in Río Muni, Equatorial Guinea. *Biological*
- 440 *Conservation*, 126, 206-215.
- 441 Espinosa, S., Branch, L.C. & Cueva, R. (2014) Road development and the geography of
- 442 hunting by an Amazonian indigenous group: consequences for wildlife
- 443 conservation, *PLoS ONE*, 9, e114916.
- 444 Fa, J.E., Seymour, S., Dupain, J., Amin, R., Albrechtsen, L. & Macdonald, D. (2006)
- 445 Getting to grips with the magnitude of exploitation: bushmeat in the Cross–Sanaga
- 446 rivers region, Nigeria and Cameroon. *Biological Conservation*, 129, 497-510.
- 447 Fa, J.E., Olivero, J., Farfán, M.Á., Márquez, A.L., Duarte, J., Nackoney, J., Hall, A.,
- 448 Dupain, J., Seymour, S., Johnson, P.J., MacDonald, D.W., Real, R. & Vargas, J.M.
- 449 (2015) Correlates of bushmeat in markets and depletion of wildlife. *Conservation*
- 450 *Biology*, 29, 805-815.

451	Foerster, S.,	Wilkie, D	S., Morell	i. G.A	Demmer, J.	. Starkey	. M.,	Telfer. P.	. Steil. M.
		, , , , , , , , , , , , , , , , , , , ,		.,,		,~~~~,	,,		,~~~,

452 & Lewbel, A. (2012) Correlates of bushmeat hunting among remote rural

453 households in Gabon, Central Africa. *Conservation Biology*, 26, 335-344.

- 454 Fragoso, J.M.V. (2004) A long-term study of white-lipped peccary (*Tayassu pecari*)
- 455 population fluctuation in northern Amazonia. Anthropogenic vs "natural" causes. In
- 456 *People in nature. Wildlife conservation in South and Central America* (eds K.
- 457 Silvius, R.E. Bodmer & J.M.V. Fragoso), pp. 286-296. Columbia University Press,
 458 New York, USA.
- 459 Gandiwa, E. (2011) Preliminary assessment of illegal hunting by communities adjacent
- 460 to the northern Gonarezhou National Park, Zimbabwe. *Tropical Conservation*
- 461 *Science*, 4, 445-467.
- Garcia, A., Salvador, T., Vargas, G. & Duponchelle, F. (2008) Patterns of commercial
 fish landings in the Loreto region (Peruvian Amazon) between 1984 and 2006. *Fish*
- 464 *Physiology and Biochemistry*, 35(1), 53-67, doi: 10.1007/s10695-008-9212-7.
- 465 Godoy, R., Undurraga, A., Wilkie, D., Reyes-García, V., Huanca, T., Leonard, W.R.,
- 466 McDade, T., Tanner, S., Vadez, V. & TAPS Bolivia Study Team (2010) The effect
- 467 of wealth and real income on wildlife consumption among native Amazonians in
- 468 Bolivia: estimates of annual trends with longitudinal household data (2002-2006).
- 469 *Animal Conservation*, 13(3), 265-274, doi: 10.1111/j.1469-1795.2009.00330.x.
- 470 Golden, C.D., Wrangham, R.W. & Brashares, J.S. (2013) Assessing the accuracy of
- 471 interviewed recall for rare, highly seasonal events: the case of wildlife consumption
- 472 in Madagascar. *Animal Conservation*, 16, 597-603, doi: 10.1111/acv.12047.
- 473 Gow, P. (2007) "Ex-Cocama": Transforming identities in Peruvian Amazonia. In Time
- 474 and Memory in Indigenous Amazonia (eds C. Fausto & M.J. Heckenberger), pp.
- 475 194-215. University Press of Florida, Gainesville, USA.

- 476 Gray, C., Bozigar, M. & Bilsborrow, R. (2015) Declining use of wild resources by
- 477 indigenous peoples of the Ecuadorian Amazon. *Biological Conservation*, 182, 270-

478 277. doi:10.1016/j.biocon.2014.12.022.

- 479 Hawken, A. & Munch, G.L. (2012) Cross-national indices with gender-differentiated
- 480 data: What do they measure? How valid are they?. *Social Indicators Research*, 111,481 801-838.
- 482 Hill, K., Hawkes, K., Hurtado, M. & Kaplan, H. (1984) Seasonal variance in the diet of
 483 Ache hunter-gatherers in Eastern Paraguay. *Human Ecology*, 12, 101-135.
- 484 INRENA (Instituto Nacional de Recursos Naturales) (2009) *Plan maestro de la Reserva*485 *Nacional Pacaya Samiria*. INRENA, Lima, Peru.
- 486 Kvist, L.P., Gram, S., Cácares, A.C. & Orem, I.B. (2001) Socio-economy of flood plain
- 487 households in the Peruvian Amazon. *Forest Ecology and Management*, 150, 175488 185.
- 489 Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E.,
- 490 Campbell, P. & Ondzeano, C. (2006) Impacts of roads and hunting on Central

491 African rainforest mammals. *Conservation Biology*, 20, 1251-1261.

- 492 Levi, T., Lu, F., Yu, D.W. & Mangel, M. (2011) The behavior and diet breadth of
- 493 central-place foragers: an application to human hunters and Neotropical game
- 494 management. *Evolutionary Ecology Research*, 13, 171-185.
- 495 Levi, T., Shepard Jr, G.H., Ohl-Schacherer, J., Peres, C.A. & Yu, D.W. (2009)
- 496 Modelling the long term sustainability of indigenous hunting in Manu National
- 497 Park, Peru: landscape-scale management implications for Amazonia. *Journal of*
- 498 *Applied Ecology*, 46, 804-814, doi: 10.1111/j.1365-2664.2009.01661.x.
- 499 Lu, F. (2007) Integration into the market among indigenous peoples: a cross-cultural
- 500 perspective from the Ecuadorian Amazon. *Current Anthropology*, 48, 593-602.

- 501 Mayor, P., El Bizri, H., Bodmer, R.E. & Bowler, M. (2017) Assessment of mammal
- 502 reproduction for hunting sustainability through community-based sampling of

species in the wild. *Conservation Biology*, 31, 912-923, doi: 10.1111/cobi.12870

- 504 Mayor, P., Pérez-Peña, P., Bowler, M., Puertas, P.E., Kirkland, M. & Bodmer, R.E.
- 505 (2015) Effects of selective logging on large mammal populations in a remote
- 506 indigenous territory in the northern Peruvian Amazon. *Ecology and Society*, 20(4),
- 507 36, doi: 10.5751/ES-08023-200436.
- 508 McSweeney, K. & Jokisch, B. (2007) Beyond rainforests: urbanisation and emigration
- 509 among lowland indigenous societies in Latin America. *Bulletin of Latin American*

510 *Research*, 26, 159-180. doi: 10.1111/j.1470-9856.2007.00218.x.

- 511 Morcatty, T.Q. & Valsecchi, J. (2015) Social, biological, and environmental drivers of
- 512 the hunting and trade of the endangered yellow-footed tortoise in the Amazon.

513 *Ecology and Society*, 20(3), 3, doi:10.5751/ES-07701-200303.

- 514 Naranjo, E.J. & Bodmer, R.E. (2007) Source-sink systems and conservation of hunted
- 515 ungulates in the Lacandon Forest, Mexico. *Biological Conservation*, 138, 412-420.
- 516 Navaro, A J., Redford, K.H. & Bodmer, R.E. (2000) Effect of hunting in source-sink

517 systems in the Neotropics. *Conservation Biology*, 14, 713-721.

- 518 Ohl-Schacherer, K., Shepard Jr, G.H., Kapla, H. & Yu, D.W. (2007) The sustainability
- 519 of subsistence hunting by Matsigenka native communities in Manu National Park,
- 520 Peru. *Conservation Biology*, 21, 1174-85.
- 521 Parry, L. & Peres, C.A. (2015) Evaluating the use of local ecological knowledge to
- 522 monitor hunted tropical-forest wildlife over large spatial scales. *Ecology and*
- 523 *Society*, 20(3), 15, doi: 10.5751/ES-07601-200315.
- 524 Patton, M.Q. (2002). *Qualitative Research and Evaluation Methods*. Sage Publications,
- 525 Thousand Oaks, USA.

- 526 Peres, C.A. & Dolman, P.M. (2000). Density compensation in neotropical primate
- 527 communities: evidence from 56 hunted and nonhunted Amazonian forests of
 528 varying productivity. *Oecologia*, 122, 175-189.
- 529 Peres, C.A. & Lake, I.R. (2003) Extent of nontimber resource extraction in tropical
- 530 forests: accessibility to game vertebrates by hunters in the Amazon Basin.
- 531 *Conservation Biology*, 17(2), 521-535, doi: 10.1046/j.1523-1739.2003.01413.
- 532 Peres, C.A & Palacios, E. (2007) Basin-wide effects of game harvest on vertebrate
- 533 population densities in Amazonian forests: implications for animal-mediated seed
- dispersal. *Biotropica*, 39, 304-315.
- 535 R Core Team (2016) R: A Language and Environment for Statistical Computing. R
- 536 Foundation for Statistical Computing, Vienna, Austria.
- 537 Richard-Hansen, C., Surugue, N., Khazraie, K., Le Noc, M. & Grenand, P. (2013)
- 538 Long-term fluctuations of white-lipped peccary populations in French Guiana.
 539 *Mammalia*, 78, 291-301.
- 540 Rist, J., Milner-Gulland, E.J., Cowlishaw, G. & Rowcliffe, M. (2010) Hunter reporting
- 541 of catch per unit effort as a monitoring tool in a bushmeat-harvesting system.

542 *Conservation Biology*. 24, 489-499. doi: 10.1111/j.1523-1739.2010.01470.x

- 543 Roos, N., Wahab, M.A., Chamnan, C. & Thilsted, S.H. (2007) The role of fish in food-
- based strategies to combat vitamin A and mineral deficiencies in developing
 countries. *American Society for Nutrition* 137, 1106-1109.
- 546 Rubin, H.J. & Rubin, I.S. (2005) *Qualitative Interviewing: The Art of Hearing Data*.
- 547 Sage Publications, Thousand Oaks, USA.
- 548 da Silva, M.N.F., Shepard Jr, G.H. & Yu, D.W. (2005) Conservation implications of
- 549 primate hunting practices among the Matsigenka of Manu National Park, Peru.
- 550 *Neotropical Primates*, 13, 31-36.

- 551 Sirén A. & Wilkie, D. (2016) The effects of ammunition price on subsistence hunting in
- 552 an Amazonian village. *Oryx*, 50, 47-55, doi: 10.1017/S003060531400026X.
- 553 Smith, A. & Wishnie, M. (2000) Conservation and subsistence in small-scale societies,
- 554 *Annual Review of Anthropology*, 29, 493-524, doi:
- 555 10.1146/annurev.anthro.29.1.493
- 556 Suarez, E., Morales, M., Cueva, R., Bucheli, V.U., Zapata-Rios, G., Toral, E., Torres, J.,
- 557 Prado, W. & Olalla, J.V. (2009) Oil industry, wild meat trade and roads: indirect
- 558 effects of oil extraction activities in a protected area in north-eastern Ecuador.
- 559 Animal Conservation, 12, 364-373.
- 560 Vasco, C. & Sirén, A. (2016) Correlates of wildlife hunting in indigenous communities
- 561 in the Pastaza province, Ecuadorian Amazonia. *Animal Conservation*, 19, 22-429.
- 562 doi:10.1111/acv.12259
- 563 Wilkie, D.S. & Godoy, R.A. (2001) Income and price elasticities of bushmeat demand

564 in lowland Amerindian societies. *Conservation Biology* 15:761-769.

- 565 Wilkie, D.S., Shaw, E., Rotberg, F., Morelli, G. & Auzel, P. (2000) Roads, development
- and conservation in the Congo Basin. *Conservation Biology*, 14, 1614-1622.
- 567 Zapata-Ríos, G., Urgil, C. & Suárez, E. (2009). Mammal hunting by the Shuar of the
- 568 Ecuadorian Amazon: Is it sustainable?. *Oryx*, 43, 375-385.
- 569 Zimmerman, B., Peres, C.A., Malcolm, J.R. & Turner, T. (2001) Conservation and
- 570 development alliances with the Kayapó of south-eastern Amazonia, a tropical forest
- 571 indigenous people. *Environmental Conservation*, 28, 10-22.
- 572

573 Biographical sketches

574

575 Maire Kirkland conducts research into the sustainable use of natural resources. Cristina

- 576 Eisenberg works on food-web relationships, sustainable natural resources use, and
- 577 ecological restoration globally, with a focus on Indigenous communities. Andy Bicerra,
- 578 Richard E. Bodmer and Pedro Mayor are involved in wildlife research and biodiversity
- 579 conservation in the Neotropics. Jan C. Axmacher explores patterns of biodiversity in
- 580 China and the UK.

Table 1. Details of interviews and harvest rates in the five Kukama-Kukamilla communities located at the mouth of the Samiria River. The amount of meat available for consumption refers to the edible portion of fish and game meat, which was calculated as 70% of biomass extracted (Hill et al., 1984; Roos et al., 2007).

Community	San Martín de Tipishca	Nuevo Arica	Bolivar	Leoncio Prado	San José de Samiria
Number of families	120	50	40	90	50
Number interviewed (%)	29 (24.2%)	28 (56.0%)	9 (22.5%)	30 (33.3%)	26 (52.0%)
Total community-level	× ,	. ,	. ,	. ,	. ,
harvest per year (t)					
Fish	679.64	222.26	359.32	327.95	151.26
Game	15.01	14.42	8.40	9.94	10.70
Total meat	694.65	236.68	367.72	337.89	161.96
Total harvest per-capita per					
year (t)					
Fish	0.94	0.74	1.50	0.61	0.51
Game	0.04	0.09	0.06	0.03	0.06
Total meat	0.98	0.83	1.56	0.64	0.57
Total meat available for					
consumption					
Per household per year	4 1 1	2 47	6 55	2 69	2.20
(t)	4.11	5.47	0.33	2.08	2.39
Per-capita per year (t)	0.68	0.58	1.09	0.45	0.40
Per-capita per day (kg)	1.88	1.59	2.99	1.22	1.09

Species			Percent househ	tage of olds (%)
Order	Scientific name	Local name	High	Low
Characiformes	Prochilodus nigricans	Boquichico	83.33	77.12
	Hoplerythrinus unitaeniatus	Shuyo	60.83	41.18
	Mylossoma duriventre	Palometa	26.67	45.00
	Hoplias malabaricus	Fasaco	26.67	28.57
	Triportheus spp.	Sardina	25.00	22.69
	Leporinus spp.	Lisa	15.83	22.69
	Pygocentrus/Serrasalmus spp.	Piraña	14.17	17.65
	Potamorhina latior	Yahuarachi	6.67	4.20
	Brycon spp.	Sabalo	5.83	5.74
	Colossoma macropomum	Gamitana	0.83	0.83
Perciformes	Satanoperca jurupari	Bujurqui vaso	15.00	23.33
	Astronotus ocellatus	Acarahuazú	9.17	26.27
	Cichla monoculus	Tucunaré	0.83	6.67
Siluriformes	Pterygoplichthys pardalis	Carachama	64.17	51.28
	Pseudoplatystoma tigrinum	Tigre zúngaro	4.17	5.83
	Pimelodus blochii	Bagre	3.33	4.17
	Pseudoplatystoma fasciatum	Doncella	3.33	2.50
	Hoplosternum spp.	Shirui	2.50	0.83
	Hypophthalmus edentatus	Maparate	0.83	1.67
	Oxydoras niger	Turushuqui	0.83	0.83
	Leiarius marmoratus	Achara	0.83	0.83
	Sorubim lima	Shiripira	0.83	0.00

Table 2. Fish species harvested by the Kukama-Kukamilla people, showing the proportion of households harvesting each species during high- and low-water seasons.

Biomass (kg) 17.33	Number of individuals
17.33	
17.33	
	0.50
2.60	0.10
1.02	0.05
13.19	0.10
3.38	0.42
1.63	0.33
2.90	0.01
1.61	0.27
1.19	0.18
0.25	0.09
0.19	0.07
0.18	0.02
0.04	0.01
0.01	0.02
0.17	0.03
7.00	0.15
1.60	0.05
2.78	0.35
1.02	0.13
1.88	0.07
0.58	0.19
0.29	0.10
0.22	0.16
0.15	0.12
0.25	0.17
0.24	0.20
0.04	0.04
	17.33 2.60 1.02 13.19 3.38 1.63 2.90 1.61 1.19 0.25 0.19 0.18 0.04 0.01 0.17 7.00 1.60 2.78 1.02 1.88 0.27 8 1.02 1.88 0.29 0.22 0.15 0.25 0.24 0.04

Table 3. Annual per-capita harvest rates of game species by the Kukama-Kukamilla people, showing the biomass and number of individuals harvested per person per year.

Table 4. Results of the multiple linear regression analyses showing the effect of village size, market exposure and season on log-transformed harvest rates and CPUE. Non-significant variables were excluded from each model.

	Estimate \pm SE	<i>t</i> -value	P-value
Community-level harvest rates			
(Intercept)	3.41 ± 0.35	9.74	< 0.000
Village size	0.01 ± 0.00	2.66	0.032
Low-water season	1.25 ± 0.26	4.80	0.002
Per-capita harvest rates			
(Intercept)	-1.52 ± 0.18	-8.61	< 0.000
Commercial	-0.54 ± 0.22	-2.44	0.045
Low-water season	1.25 ± 0.22	5.76	< 0.001
CPUE			
(Intercept)	-0.80 ± 0.14	5.73	< 0.001
Commercial	-1.10 ± 0.17	-6.27	< 0.001
Low-water season	1.61 ± 0.17	6.78	< 0.001