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2 **Running Header:** Seasonal reproduction and hunting of pacas

3

4 **Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions**
5 **with rainfall, fruiting, and sustainable hunting**

6

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32 The resilience of a given species to hunting is conditioned by the effect of potential threats
33 upon the more sensitive periods in its life history, such as when animals are breeding. We
34 investigated the environmental drivers of breeding seasonality in the lowland paca (*Cuniculus*
35 *paca*), and the potential impact of hunting on the species. As part of a participative study with
36 hunters in 2 Amazonian sites, we obtained reproductive organs of pacas as well as
37 information on the hunters' daily wild meat extraction. Using data on rainfall, river water
38 level, and fruiting phenology from the 2 study sites, we applied generalized additive models
39 (GAMLSS) to examine the effect of climatic and environmental factors on paca reproduction.
40 Forest fruiting was directly linked to higher pregnancy rates in pacas, and when lactation and
41 weaning of offspring mostly occurred. Hunting was highly seasonal in all studied years and
42 positively correlated with higher levels of river water. The coincidence between hunting
43 patterns and paca reproductive cycles during the wet season resulted in more pregnant
44 females being harvested. In addition to the known slow reproductive rate of pacas, the
45 disproportionate offtake of pregnant females may affect the long-term sustainability of
46 hunting of this species. Reducing hunting during the flooded season may not be feasible
47 because the lowland paca provides most of wild meat consumed by thousands of rural
48 Amazonians during this period. However, options to offset the negative effects of killing of
49 pregnant females could include the zoning of hunting areas or encouraging hunters to target
50 primarily males. Our results indicate that strategies for the sustainable harvest of paca and

51 other heavily hunted Amazonian mammals should consider the interaction between the
52 species' reproductive cycles and hunting by local people in order to enhance conservation
53 and management efforts.

54

55 Key words: conception dates, forest phenology, game species, hunter participation,
56 management, pregnancy rates, rainfall patterns, reproduction, Rodentia, wildlife

57

58 A resiliência de uma espécie à caça é condicionada pela sua capacidade reprodutiva
59 intrínseca e pelo efeito de potenciais ameaças durante os períodos mais sensíveis de sua
60 história de vida, como o período reprodutivo. Neste trabalho, nós investigamos os fatores
61 ambientais que determinam a sazonalidade reprodutiva da paca (*Cuniculus paca*) e o
62 potencial impacto da caça sobre espécie. Em um estudo participativo de 15 anos em duas
63 áreas da Amazônia, obtivemos órgãos reprodutivos de pacas doados voluntariamente por
64 caçadores, bem como informações sobre seus padrões diários de caça. Usando informações
65 sobre precipitação, nível d'água dos rios e fenologia de frutificação, nós aplicamos modelos
66 aditivos generalizados (GAMLSS) para examinar o efeito de fatores climáticos e ambientais
67 na reprodução da paca. A precipitação esteve positivamente ligada a uma maior frutificação,
68 que por sua vez foi correlacionada com maiores taxas de prenhes da paca e com os períodos
69 de lactação e desmame da prole. A caça de paca foi altamente cíclica ao longo dos anos e
70 positivamente associada aos níveis d'água mais elevados. A convergência entre os padrões de
71 caça e os ciclos reprodutivos de paca resulta na extração de um grande número de fêmeas
72 grávidas. Juntamente com a lenta taxa de reprodução da espécie, a captura desproporcional de
73 fêmeas grávidas pode afetar a sustentabilidade do uso da paca. Reduzir a caça durante os
74 períodos de inundação pode não ser viável, pois a paca é a espécie responsável por fornecer
75 grande parte da carne silvestre consumida por milhares de moradores rurais da Amazônia

76 neste período. No entanto, ações para compensar os efeitos negativos da extração de pacas
77 grávidas poderiam incluir o zoneamento de áreas de caça ou o incentivo aos caçadores em
78 abater preferencialmente machos. Nossos resultados indicam que estratégias para a extração
79 sustentável da paca e outras espécies cinegéticas amazônicas devem considerar a interação
80 entre a reprodução e a caça pela população local, a fim de melhorar as ações de conservação e
81 manejo no bioma.

82

83 Palavras-chave: datas de concepção, fenologia florestal, espécies cinegéticas, coleta
84 participativa, manejo, taxas de prenhes, padrões de chuva, reprodução, Rodentia, vida
85 silvestre

86

87 In high latitudes, where climatic variability between seasons is greatest, most species produce
88 a large number of offspring in a short period of time, most of which do not survive (Bronson
89 1985). By contrast, in more stable environments with less seasonal variation, such as tropical
90 forest regions, species generally produce a constant, low number of offspring over the year
91 (McNaughton 1975). However, in the Amazon basin, the extreme variation in river levels,
92 caused by seasonal meltwater in the Andes or rainfall, affects food availability (particularly
93 tree fruits) to such an extent that frugivorous mammals may exhibit a greater than expected
94 reproductive seasonality for this environment (Dubost et al. 2005). Seasonal patterns in water
95 levels also determine patterns of hunting and fishing by humans (Endo et al. 2016).

96 Animal populations are regulated by factors that impact mortality and recruitment
97 (Caughley 1977). Understanding the population dynamics of exploited species is essential to
98 determine sustainable harvest rates for wildlife populations. Harvesting individuals can have
99 direct effects on the growth rate of a population by increasing mortality rates. There is
100 increasing evidence that harvesting can also have indirect effects on population growth. For

101 instance, harvest can disrupt the sex and age structure of a population, which can in turn
102 affect fecundity rates (Milner et al. 2007; Bunnefeld et al. 2009). Furthermore, sex-skewed
103 harvesting can have potentially deleterious effects on long-term fecundity (defined as the
104 number of young born) and lead to population collapse, as shown for ungulates (Ginsberg
105 and Milner-Gulland 1994; Freeman et al. 2014). In addition, overhunting of females in
106 seasonally breeding animals, during periods when more females are pregnant, may negatively
107 influence the population dynamics of the species.

108 In this paper, we evaluate how hunting may affect the population dynamics of the
109 lowland paca (*Cuniculus paca*). The paca is a large, frugivorous caviomorph rodent that
110 occurs throughout the Neotropics, inhabiting primarily broadleaf forests from east-central
111 Mexico to northern Argentina. (Collet 1981; Pérez 1992; Aquino et al. 2009; Goulart et al.
112 2009). Studies to date, in primary broadleaf forest, suggest that pacas occupy relatively small
113 home ranges (Marcus 1984; Beck-King et al. 1999), and are patchily distributed in mosaic
114 landscapes with scattered resources (Marcus 1984; Beck-King et al. 1999; Ulloa et al. 1999).
115 Pacas feed mostly on fruits and seeds, and occasionally consume leaves and flowers (Beck-
116 King et al. 1999; Dubost 2017).

117 Pacas are of conservation and management interest throughout their geographic range,
118 as a popular game species for people (e.g., Read et al. 2010; El Bizri et al. 2015, 2016;
119 Gutiérrez-Granados 2015; Mayor et al. 2015), an important prey of large carnivores, and as
120 seed dispersers (Dubost and Henry 2006; Aquino et al. 2009; Foster et al. 2016). However,
121 there is concern that current levels of hunting may be unsustainable, as observed in several
122 Amazonian sites (e.g., Zapata-Ríos et al. 2009; Valsecchi et al. 2014). Given the importance
123 of the paca as a source of protein to human residents of tropical forests, identifying the
124 factors that may affect paca numbers remains fundamental.

125 Here, in 2 sites in Amazonian Peru and Brazil, we first assess how environmental
126 factors such as rainfall patterns affect fruit availability, and in turn show how this correlates
127 with the reproductive seasonality of pacas. We then assess the impact of hunting rates during
128 the different phases of the reproductive cycle of pacas using data gathered from a 15-year
129 participatory hunting study for the 2 study sites.

130

131

MATERIALS AND METHODS

132 *Study sites.*— The Yavarí-Mirín River (YMR; 04°19'53" S, 71°57'33" W) is located
133 in the western Peruvian Amazon, encompassing 107,000 ha of continuous upland forests
134 containing a single indigenous community of 307 inhabitants (Fig. 1). The Amanã
135 Sustainable Development Reserve (ASDR; 01°54'00" S, 64°22'00" W) is a 2,313,000-ha
136 reserve of predominantly upland forests in the central Brazilian Amazon, between the Negro
137 and Japurá rivers. Approximately 4,000 riverine people inhabit 23 communities and some
138 isolated settlements within this reserve (Fig. 1). In both study sites, local communities rely on
139 agriculture for income and on hunting and fishing for subsistence. River water levels at both
140 sites change seasonally, varying up to 12 m between the dry and flood peaks (Ramalho et al.
141 2009). Climate in both study sites is typically equatorial with annual temperatures ranging
142 between 22°C and 36°C, relative humidity of 80%, and an annual rainfall of 1,500 – 3,000
143 mm.

144 *Water level and rainfall.*— For the YMR, we calculated monthly average river water
145 level (as meters above sea level – m.a.s.l.) and rainfall (in mm) on the Yavarí River, from
146 data provided by a Brazilian National Water Agency hydrological station, c. 50 km from the
147 study site (HidroWeb, Estirão do Repouso station, rainfall: 1962 – 1999, water level: 1980 –
148 2017, <http://www.snirh.gov.br/hidroweb/>). In the ASDR, we used data on average rainfall
149 (mm) for the Tefé municipality, c. 90 km from the study area, from information also provided

150 by the Brazilian National Water Agency (HidroWeb, Tefé station, 2005 – 2017,
151 <http://www.snirh.gov.br/hidroweb/>). We used data on river water levels from the Mamirauá
152 Sustainable Development Institute for the Amanã Lake station inside the ASDR (1990 –
153 2018, [https://mamiraua.org.br/pt-br/pesquisa-e-
154 monitoramento/monitoramento/fluviometrico/](https://mamiraua.org.br/pt-br/pesquisa-e-monitoramento/monitoramento/fluviometrico/)).

155 *Ripe fruit availability.*— We determined annual changes in ripe fruit availability, the
156 main item in the diets of pacas (Dubost et al. 2005), by monitoring tree fruit abundance in 3
157 transects between March 2004 and February 2005. Two transects, started at random points,
158 were in upland forests in the YMR, and a third transect was located in *aguajal*, upland swamp
159 forest dominated by palms. All transects were 5 m wide except one in the upland forest,
160 which was 20 m wide (Pitman et al. 2003). We tagged and identified every tree of a diameter
161 at breast height (DBH) >10 cm, as well as every vine or liana of DBH >7 cm (Ayres 1986).
162 We marked plants until the rate of discovery of new species plateaued (Sutherland 2000),
163 which determined the length and area of each transect. Starting mid-month, we observed the
164 canopy of each tagged tree or vine once per month with binoculars and a small telescope,
165 recording the presence or absence of ripe fruits in each sampled individual plant. Because
166 fruits of the moriche palm (*Mauritia flexuosa*) constitute an important part of the diet of
167 pacas (Mendieta-Aguilar et al. 2015), we also obtained more detailed fruiting data from the
168 38 individuals found within the transects and analyzed it independently.

169 *Paca reproduction and hunting.*— We trained local hunters in the YMR community
170 and in 5 ASDR communities to remove all abdominal and pelvic organs from hunted
171 specimens and to store these materials in buffered 4% formaldehyde solution (v/v). From
172 2000 to 2015, local hunters collected and voluntarily donated genitalia from 300 female pacas
173 (212 in the YMR and 88 in the ASDR), each labeled with the hunting date. Since hunters do
174 not consume these organs, we avoided encouraging additional mortality to supply our study.

175 In parallel, between 2000 and 2015 in the YMR, and between 2002 and 2015 in the ASDR,
176 hunters recorded all hunted pacas, including sex and hunting date. In each monitored
177 community in YMR and ASDR, local hunters were provided with datasheets in which they
178 voluntarily recorded information on their daily hunting events. To ensure data were
179 accurately collected, we conducted regular workshops and meetings (at least once per year)
180 with all data providers and members of the participating communities. In this study, we only
181 used the data for hunted females.

182 *Data analysis.*— We removed the conceptuses from all pregnant females. Using a
183 metal caliper (maximum 300 mm) and a tape measure (1.0 mm accuracy), we measured the
184 crown-rump length and longitudinal length of each embryo or fetus, from rostral edge of nose
185 to distal portion of the tail. Conception dates were determined by backdating the date of
186 collection each embryo or fetus from their estimated age, using the age formula for paca
187 fetuses in El Bizri et al. (2017). Predicted parturition dates were estimated by summing a
188 standard gestation length of 149 days (Guimarães et al. 2008) to the derived conception dates.
189 We then calculated the monthly number and percentage of conceptions and parturitions
190 during the study period. Hunting data on females collected by local people were also used to
191 calculate the monthly percentage of female pacas hunted in each site within each monitored
192 year (hereafter known as hunting rates). Additionally, we estimated the pregnancy period
193 (from conception to parturition dates) for each paca, and summed the cumulative number of
194 pregnant pacas per month to obtain a monthly percentage of pregnant females among all
195 collected samples in a year (hereafter known as pregnancy rate). We also estimated the
196 monthly percentage of weaned offspring by summing a standard lactation length of 21 days
197 to the parturition dates, which correspond to the period after which the offspring, although
198 still suckling, starts eating solid food (Collett 1981). In addition, we calculated the average
199 longitudinal length of the embryos or fetuses per month in each locality.

200 We applied generalized additive models for location, scale, and shape (GAMLSS)
201 (Stasinopoulos and Rigby 2007) to assess the relationship between climate, fruiting, paca
202 reproductive events, and hunting. By using GAMLSS, it is possible to test across a wide set
203 of distribution families, ensuring the best fit to the data is selected. Analyses were conducted
204 in 3 sets using a theoretical framework of likely direct relationships between the variables. In
205 set (1), we evaluated the relationship between monthly rainfall (predictor variable) and
206 monthly fruiting percentage in the 3 YMR environments. In set (2), we evaluated the
207 relationship between monthly fruiting percentage in the 3 environments (predictor variables)
208 and paca reproductive events (percentage of conceptions, parturitions, and weaning, and
209 pregnancy rates) for the YMR; in this second set, we also tested rainfall as a predictor
210 variable for conceptions in both areas (YMR and ASDR), since this factor has been reported
211 as a possible cue for conceptions in several mammal species. In set (3), we evaluated the
212 relationship between river water level and paca reproductive events (predictor variables) with
213 hunting rates. For the latter, we calculated the monthly percentage of hunted females in each
214 year in both areas and related these values with the monthly average water level and
215 percentage reproductive events, which were considered constants among months,
216 independently of the year.

217 We tested all combinations of predictor variables in each set in linear or non-linear
218 forms using different distribution families. Final models were selected based on Δ AIC values,
219 i.e., the difference between the value of Akaike's information criterion (AIC) for the model
220 being evaluated and the model with the lowest AIC value (Burnham and Anderson 2004);
221 Δ AIC values smaller than 2 indicated models with good support. Among these models, we
222 chose the simplest one as final, i.e., the model with fewest degrees of freedom and with
223 fewest predictor variables in the model. We used R 3.3.3 software (R Core Team 2017) for

224 all statistical analyses. GAMLSS were run using the *gamlss* R-package. Values are expressed
225 as the mean \pm standard deviation ($\bar{X} \pm SD$).

226 *Compliance.*— All research followed guidelines of the American Society of
227 Mammalogists for the ethical use of wild animals in research (Sikes et al. 2016) and was
228 conducted in compliance with the research protocol approved by the Research Ethics
229 Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna
230 Silvestre from Peru (License 0229-2011-DGFFS-DGEFFS), by the Instituto Chico Mendes
231 for Biodiversity Conservation from Brazil (License SISBIO No 29092-1), and by the
232 Committee on Ethics in Research with Animals of the Federal Rural University of the
233 Amazon (UFRA CEUA protocol 007/2016).

234

235 RESULTS

236 *Ripe fruit availability.*— We sampled 589 trees and vines in 8,970 m² of upland
237 forests, and 386 trees and vines in 5,150 m² of swamp forests. Fruiting patterns in the YMR
238 varied according to habitat type. In upland forests, fruiting trees were present throughout the
239 year, with peaks in March (6.62% plants fruiting) and December (4.68% plants fruiting; Fig.
240 2). In swamp forests, fruiting peaked between February and May (6.12 \pm 0.83% plants
241 fruiting), with no trees fruiting in September and October. *Mauritia flexuosa* showed marked
242 fruiting during the low rainfall period (May - August), with the highest number of fruiting
243 trees recorded in June (34.21%); no fruits were observed during the remaining months of the
244 year (Fig. 2). Upland forest fruiting was positively correlated with rainfall (Fig. 3, Table 1),
245 but there was no correlation between *M. flexuosa* fruiting and rainfall in swamp forest (Table
246 1).

247 *Paca reproductive seasonality.*— There were 157 (52.3%) pregnant pacas among all
248 sampled females, 100 (47.2%) in the YMR and 57 (64.8%) in ASDR (Fig. 4). Average fetal

249 length was 11.30 ± 10.58 cm in the YMR and 17.43 ± 9.74 cm in the ASDR, with a
250 significant difference between sites ($t_{155} = 3.59$, $P < 0.01$). Paca reproductive events occurred
251 during different periods of the year in the 2 study sites. In YMR, conceptions occurred
252 mainly between October and January (50.0%), while parturitions primarily took place
253 between March and June (49.0%). In ASDR, most conceptions occurred between March and
254 June (45.6%), while most parturitions happened between August and November (42.1 %; Fig.
255 5). Nevertheless, conceptions and parturitions occurred throughout the year in both sites.
256 There was a positive relationship between conceptions and rainfall in both study sites (Figs.
257 6A and B), but there was a negative relationship between conceptions and fruiting in upland
258 forests in the YMR (Fig. 6C; Table 1). Pregnancy rates were positively associated with
259 fruiting in upland forest (Fig. 6D), while the higher weaning rates were related to higher
260 fruiting periods in swamp forest (Fig. 6E) and of *M. flexuosa* (Fig. 6F, Table 1). On the other
261 hand, there was no relationship between parturition and fruiting in any environment (Table
262 1).

263 *Hunting vulnerability of pregnant pacas.*— A total of 803 hunted paca females were
264 recorded in the communities, 288 in the YMR and 515 in the ASDR. Hunting rates varied
265 between months, which were cyclical along the years (Figs. 7A and B) and showed a positive
266 relationship with the river water level in both study sites (Figs. 7C and D, Table 1). A strong
267 positive relationship between hunting rates and pregnancy rates was observed (Figs. 7F and
268 G, Table 1). There were no relationships between conceptions, parturitions, and weaned
269 offspring and hunting rates (Table 1).

270

271

DISCUSSION

272

273

Paca reproductive seasonality and fruit availability.— Although pregnant females
were present year-round in our study sites, most pregnancies occurred during periods of

274 greater fruit availability in upland forests, when rainfall was highest. The greater food supply
275 during this period can sustain larger numbers of pregnant females. When most females are in
276 their last third of gestation, a period of greatest absolute fetal growth and when pregnant
277 individuals demand more energy, fruit availability is, in fact, at its peak. A similar pattern has
278 been observed for the ring-tailed coati (*Nasua nasua*) where the gestation period,
279 concentrated between November and March, coincided with greater fruit availability in
280 upland and swamp forests in the YMR (Mayor et al. 2013a). However, mammals with less
281 selective diets are aseasonal breeders, as in the case of the white-lipped peccary (*Tayassu*
282 *pecari*), collared peccary (*Pecari tajacu*), and the red brocket deer (*Mazama americana*)
283 (Mayor et al. 2009, 2010, 2011), because these species consume green leaves, insects, and
284 small vertebrates when fruit is less available (Dubost and Henry 2017). This pattern has also
285 been confirmed by Dubost and Henry (2017) in French Guiana, who showed that mammals
286 that consume more fruits were highly seasonal breeders.

287 *Changing energy demands and seasonality in food supply.*— There is evidence from
288 Amazonia that a seasonal increase in rainfall triggers fruit maturation in several habitat types,
289 including non-flooded forests (Haugaasen and Peres 2005). Since rainfall and river water
290 levels vary in different regions of the Amazon, reproductive events of the paca occur at
291 different phases of the year in each of our studied sites, according to local variations in
292 climate and fruit production. Paca reproduction is therefore plastic and opportunistically
293 seasonal (Mayor et al. 2013b). Thus, for fruit-dependent species, rainfall, in contrast to
294 photoperiod, may drive conceptions to take place some months prior to fruit ripening, and
295 pregnancies and births will coincide with the period of higher fruit abundance. The
296 observation made by Dubost and Henry (2006) that non-pregnant pacas consumed less seeds
297 than pregnant animals also suggests that conceptions occur during periods of low food
298 availability so that pregnancies mostly occur during periods of higher fruit and seed

299 availability. Our results also show that the greatest number of conceptions occurred when
300 fruit availability in upland forests was low; pregnant pacas could take advantage of the
301 subsequent periods of greater food supply. Similarly, in free-ranging, provisioned rhesus
302 macaques (*Macaca mulatta*) on islands in Puerto Rico, more conceptions occurred during the
303 spring rainfall period, just before the main tree-fruiting season (Rawlins and Kessler 1985).

304 In Amazonia, swamp forest species and *M. flexuosa* in particular (the most important
305 source of food during the drought period) play a major role in sustaining lactating females
306 and their young, which start weaning during the low-water period. Since during lactation
307 females consume up to 5 times more food than before pregnancy (Randolph et al. 1977), the
308 availability of ripe fruits during this period is of extreme importance. For several species of
309 flying foxes (*Pteropus* spp.), O'Brien (1993) showed that lactation and offspring weaning
310 occur during periods when fruit supply is at its peak. In addition, Lee et al. (2017) showed
311 that giraffe (*Giraffa camelopardalis*) calves born during the dry season in Tanzania had a
312 higher survival probability due to the greater energy reserves accumulated by mothers during
313 the rainy season as well as the higher protein concentration of available browse during the
314 late dry-season rains.

315 *Hunting and reproduction in quarry species.*— Different prey can cope with human
316 harvest according to their population dynamics and biological capacity (Cardillo et al. 2005),
317 but their patterns of reproduction reflect their response to environmental and human
318 disturbance. Predator–prey systems often co-evolve slowly through generations by the action
319 of natural selection, with the appearance of phenotypical and behavioral traits in prey species
320 that avoid their extinction (Kooijman and Lika 2014). However, the current reproductive
321 strategies in wild species are not adapted to the typically more intensive levels of human
322 predation, especially when hunting is directly impacting pregnant females and affecting the
323 species' recruitment potential.

324 Water levels and hunting rates were shown to have a similar cyclical pattern over the
325 period of 15 years for which data were available. Other studies in the Amazon basin have
326 also demonstrated that hunters maximize their captures by taking into account seasonal water
327 level changes (Kvist et al. 2001; Endo et al. 2016). This temporal convergence between
328 heavier hunting and pregnancies in pacas is thus likely to adversely impact the species'
329 population dynamics. A probable indication that hunting of pregnant paca females during
330 high-water periods may affect populations of the species is available for the ASDR, where
331 Valsecchi et al. (2014) demonstrated that paca hunting is unsustainable and the species'
332 abundance at this site significantly dropped over an 8-year period.

333 *Management implications.*— Pacas provide the largest proportion of wild meat
334 consumed by local populations and even urban dwellers in the Amazon (Bodmer and Lozano
335 2001; Suárez et al. 2009; van Vliet et al. 2015). However, the species has a relatively low
336 reproductive output, in which females only produce 1 young per pregnancy (Mayor et al.
337 2013b; El Bizri et al. 2017). The results presented here highlights the necessity for
338 developing sustainable harvest strategies that are compatible with the target species' life
339 history and their reproductive patterns. These strategies could include focusing hunting
340 efforts on males or reducing hunting during the pregnancy season. However, avoiding
341 hunting pacas during high water levels may not be possible for hunters. During the flooded
342 period, fishing becomes difficult and hunting becomes the main source of meat supply during
343 this period (Valsecchi et al. 2014; Endo et al. 2016), thus making it unlikely for a shift away
344 from hunting pacas during the wet season. On the other hand, since male pacas can fertilize
345 several females, hunting males exclusively during the high-water period, when pregnant
346 females are more common, is feasible since rural Amazonian hunters pursue pacas by
347 “spotlighting” (Valsecchi et al. 2014), thus permitting the identification of the sex of the
348 animal and even the pregnancy stage of females (H. R. El Bizri, pers. obs.).

349 Another strategy to improve the state of hunted paca populations is to encourage the
350 use of rotating hunting areas over the years or to protect areas during the hunting season that
351 could act as refugia for females. This strategy would create a source-sink system where
352 protected grounds would function as sources of individuals to repopulate areas depleted by
353 hunting. This strategy has already been advocated as efficient to conserve species such as the
354 culpeo fox (*Pseudalopex culpaeus*) in the Argentine Patagonia (Novaro et al. 2005) as well as
355 ungulates in the Neotropics (Naranjo et al. 2001; Naranjo and Bodmer 2007). A similar
356 approach was effectively applied to recover giant Arapaima (*Arapaima gigas*) populations by
357 encouraging community-based source-sink schemes; this system is now successfully applied
358 throughout the Amazon (Campos-Silva et al. 2017). Here, we argue that source-sink systems
359 could be equally applied for pacas. However, as all systems, these also need to be
360 continuously monitored and adapted especially because the demand for paca meat is likely to
361 increase in line with human population growth. Thus, additional measures such as setting
362 quotas of the paca population that can be harvested per family, hunter, or community may be
363 needed. Finally, since palm species are essential for pacas, and probably other Amazonian
364 species, to achieve their highest reproductive potential, actions focused on conservation of
365 swamp forest palm species, which are largely exploited by humans (Peters et al. 1989; Rull
366 and Montoya 2014), are also critical.

367 Due to the fact that most hunting in Amazonia is determined by the annual variation
368 in river water level, we argue that the impact we have observed in pacas could be mirrored in
369 other species, and hence might affect the sustainability of wild meat, so vital for numerous
370 inhabitants. Accordingly, strategies that ensure the sustainability of hunted Amazonian
371 species must be based on reproductive information to minimize the impact on their
372 populations when they are most vulnerable.

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FIGURE LEGENDS

FIGURE 1. Location of the 2 study sites (YMR: Yavari-Mirin River, ASDR: Amanã Sustainable Development Reserve) in Amazonia and the communities participating in the monitoring of hunting and collection of biological material on lowland pacas (*Cuniculus paca*).

FIGURE 2. Trends in (A) rainfall (dashed line) and percentage of trees bearing fruits in upland forests (solid line) and swamp forest (solid line); and (B) rainfall (dashed line) and percentage of *M. flexuosa* trees bearing fruits (solid line) along the year in the Yavari-Mirin River, western Amazonia.

FIGURE 3. Relationship between rainfall (mm) and percentage of trees bearing fruits in upland forests in the Yavari-Mirin River, western Amazonia. The gray area represents 95% confidence intervals. The response variable is plotted on the y-axis in a scale of variation around the mean ($\mu = 0$) calculated from the original data used to build the model.

FIGURE 4. Number and percentage of lowland paca (*Cuniculus paca*) samples that included a uterus showing signs of pregnancy, collected in each month over the monitoring years in the Amanã Sustainable Development Reserve (ASDR) and Yavari-Mirin River (YMR), Amazonia.

FIGURE 5. Trends in (A, B) the percentage of paca conceptions (dashed gray lines) and parturitions (solid black lines); and (C, D) average river water level (dashed lines) and percentage of pregnant female pacas (solid lines) along the year in the Amanã Sustainable Development Reserve (ASDR) and Yavari-Mirin River (YMR), Amazonia.

FIGURE 6. Relationship between (A) rainfall and the percentage of paca conceptions in the Amanã Sustainable Development Reserve, central Amazonia; (B) rainfall and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (C) percentage of trees bearing fruits in upland forest and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (D) percentage of trees bearing fruits in upland forest and pregnancy rate in the Yavarí-Mirín River, western Amazonia; (E) percentage of trees bearing fruits in swamp forest and percentage of weaned offspring, and (F) percentage of *M. flexuosa* trees bearing fruits and percentage of weaned offspring in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% confidence intervals. Response variables are plotted on the y-axis in a scale of variation around the mean ($\mu = 0$) calculated from the original data for models with a single predictor variable, and from partial residuals for models including more than 1 predictor variable.

FIGURE 7. Temporal trends of the river water level and hunting rates (monthly percentage of hunted females within each year) in the (A) Amanã Sustainable Development Reserve, and (B) Yavarí-Mirín River, in Amazonia. Relationship between river water level and hunting rates in the (C) Amanã Sustainable Development Reserve and (D) Yavarí-Mirín River, in Amazonia. Relationship between pregnancy rate and hunting rates in the (E) Amanã Sustainable Development Reserve and (F) Yavarí-Mirín River, in Amazonia. The gray area represents 95% confidence intervals. Response variables are plotted on the y-axis in a scale of variation around the mean ($\mu = 0$) calculated from partial residuals of the models.

TABLES

Table 1. Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, Δ AIC in relation to the null model (Δ AIC null), and generalized R^2 . Non-linear effects were fit using cubic spline (*cs*) functions provided by *gamlss* R-package. Families of distributions are represented by log-Normal (LOGNO), Normal (NO), Zero-Adjusted Gamma (ZAGA), Gamma (GA), Box-Cox t (BCTo), inverse Gaussian (IG), Gumbel (GU), and Inverse Gamma (IGAMMA). Generalized R^2 were calculated using the function *Rsq* of the *gamlss* package. Null models are indicated by 1.

Best fitted model ^a		Estimate	P-value	Family of distribution	Δ AIC null	Generalized R^2
Response variables	Predictor variables					
Yavarí-Mirín River						
Fruiting						
% plants fruiting U.F.	<i>cs</i> (rainfall)	0.0068		LOGNO	5.45	62
% plants fruiting S.F.	1	-		NO	1.23	
% plants fruiting <i>M.f.</i>	1	-		ZAGA	0.87	
Paca reproductive events						
% conceptions	rainfall	0.0083	0.011	LOGNO	3.97	48.5
	% plants fruiting U.F.	-0.2147	0.027			
% parturitions	1			IG	1.22	
% weaned offspring	% plants fruiting S.F.	0.6945	0.009	GU	11.95	73.5
	% plants fruiting <i>M.f.</i>	0.0972	0.041			
pregnancy rate	<i>cs</i> (plants fruiting U.F.)	0.0734	0.007	IGAMMA	5.6	67
Paca hunting						
hunting rates	water level	0.0541	0.033	ZAGA	6.02	6.73
	pregnancy rate	0.2239	0.003			
Amanã Reserve						
Paca reproductive events						
% conceptions	<i>cs</i> (rainfall)	0.0333	0.001	RG	3.97	53.6
Paca hunting						
hunting rates	water level	0.102	<0.001	ZAGA	7.22	29.1
	pregnancy rate	0.2223	<0.001			

^aabbreviations for plants fruiting – U.F.: upland forest; S.F.: swamp forest; *M.f.*: *Mauritia flexuosa*.

FIGURE LEGENDS

FIGURE 1. A map showing the location of the two study sites (YMR: Yavarí-Mirín River, ASDR: Amanã Sustainable Development Reserve) in Amazonia and the communities participating in the hunting monitoring and biological material collection on lowland pacas (*Cuniculus paca*).

FIGURE 2. Trends in (A) rainfall (dashed dark blue line) and percentage of fruiting trees in upland forest (solid green line) and swamp forest (solid orange line); and (B) rainfall (dashed dark blue line) and percentage of *M. flexuosa* fruiting trees (solid brown line) along the year in the Yavarí-Mirín River, Western Amazonia.

FIGURE 3. Relationship between rainfall (mm) and percentage of fruiting trees in upland forests (U.F.) in the Yavarí-Mirín River, Western Amazonia.

FIGURE 4. Trends in (A, B) the percentage of paca conceptions (dashed grey lines) and parturitions (solid black lines); and (C, D) river water level (dashed blue lines) and percentage of pregnant paca females (solid red line) along the year in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), in Amazonia.

FIGURE 5. Relationship between (A) rainfall and the percentage of paca conceptions in the Amanã Sustainable Development Reserve, Central Amazonia; (B) rainfall and percentage of paca conceptions, (C) percentage of fruiting trees in upland forest (U.F) and percentage of paca conceptions, (D) percentage of fruiting trees in upland forest (U.F) and pregnancy rate, (E) percentage of fruiting trees in swamp forest (S.F) and percentage of weaned offspring,

and (C) percentage of fruiting trees of *M. flexuosa* (M.f) and percentage of weaned offspring in the Yavarí-Mirín River, Western Amazonia.

FIGURE 6. Temporal trends of the river water level and monthly percentage of hunted females along the years in the (A) Amanã Sustainable Development Reserve, and (B) Yavarí-Mirín River, in Amazonia. Relationship between river water level and monthly percentage of hunted females in the (C) Amanã Sustainable Development Reserve and (D) Yavarí-Mirín River, in Amazonia. Relationship between pregnancy rate and monthly percentage of hunted females in the (E) Amanã Sustainable Development Reserve and (F) Yavarí-Mirín River, in Amazonia.

Fig. 1

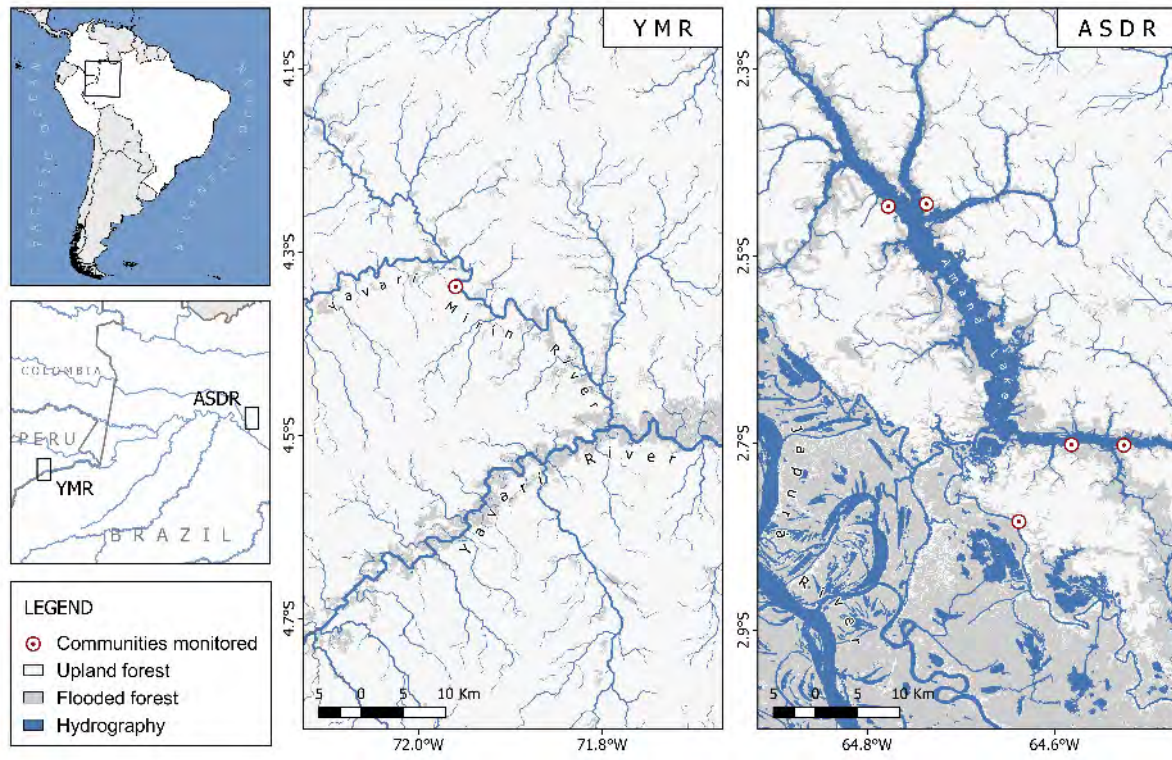


Fig. 2

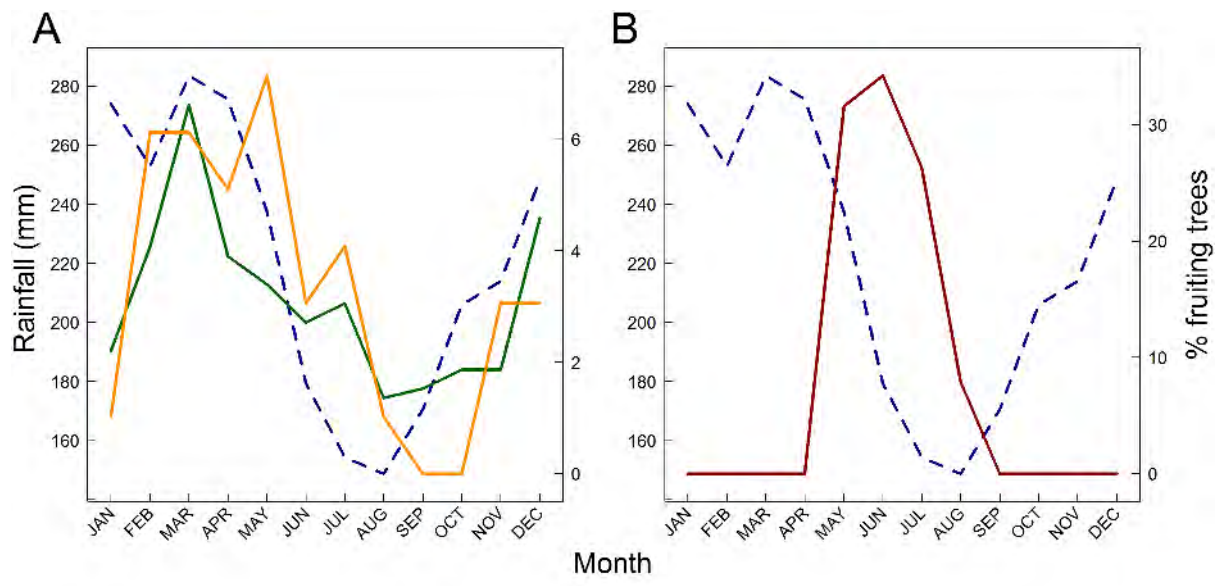


Fig. 3

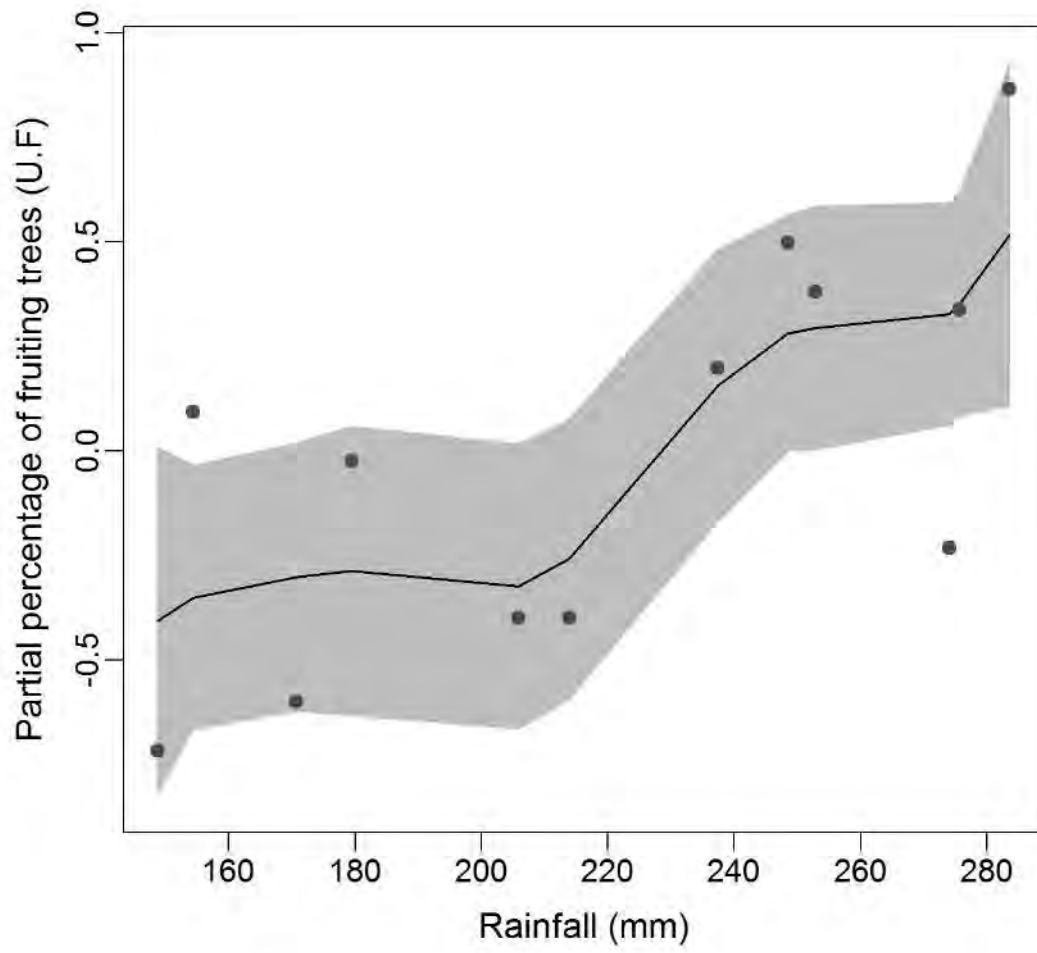


Fig. 4

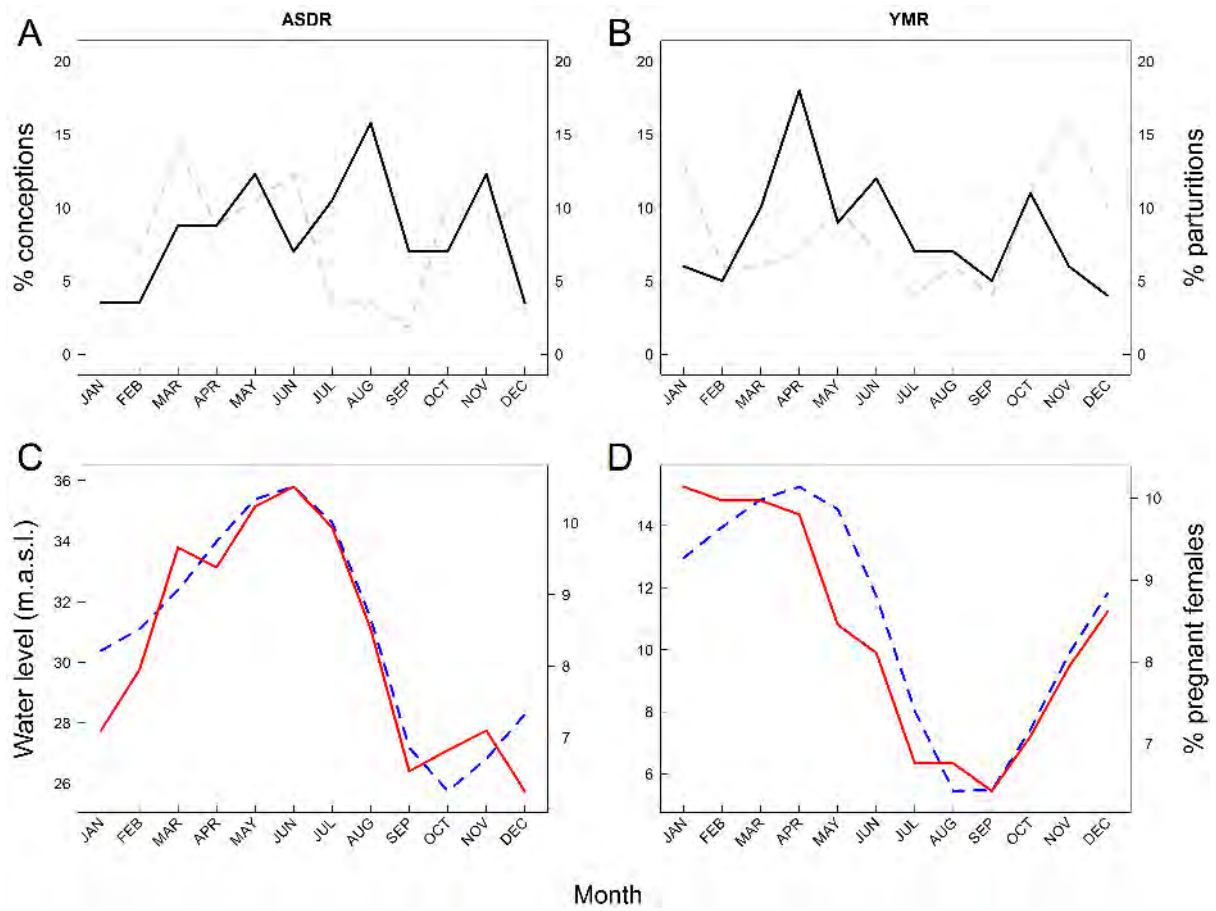


Fig. 5

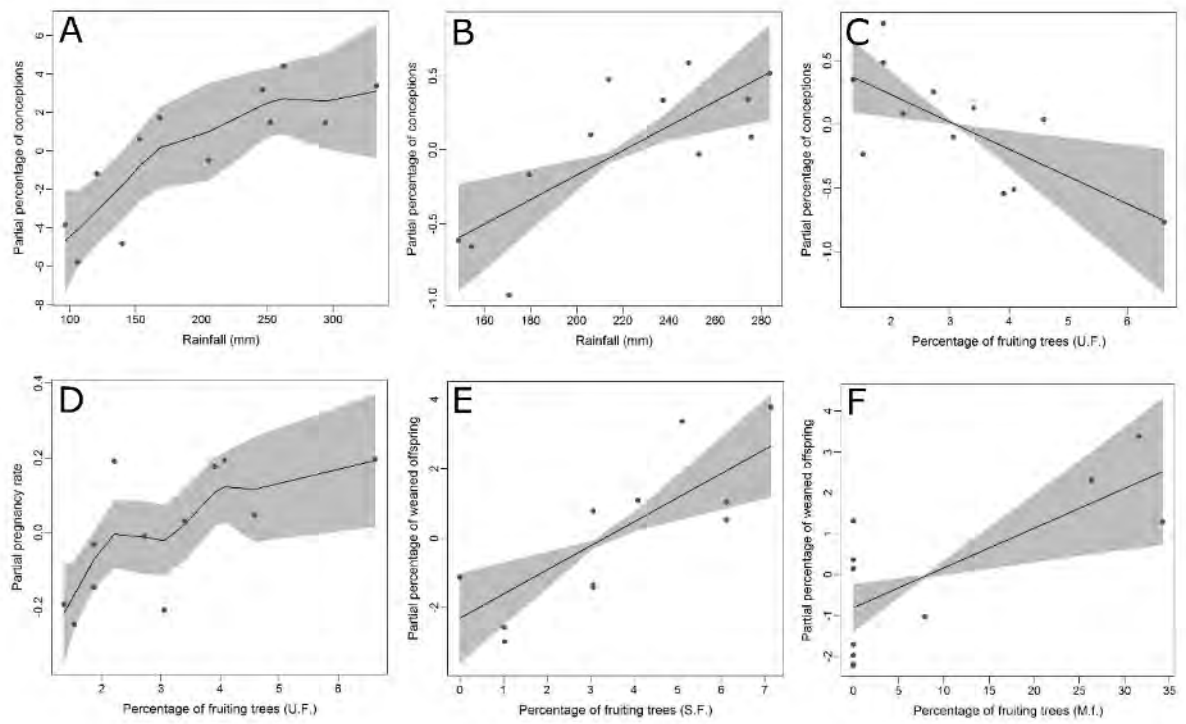


Fig. 6

